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# A REVISION OF THE GENUS *BELGRANDIA*, WITH THE DESCRIPTION OF A NEW SPECIES FROM FRANCE (CAENOGASTROPODA: HYDROBIIDAE)

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## ABSTRACT

A new species of the hydrobiid genus *Belgrandia* Bourguignat, 1869, *B. gfrast,* nov. sp., from the nature reserve Petite Camargue Alsacienne in France is described. In order to define the new species, it was necessary to investigate the syntype series or topotypes of the known nominal species. This revision is based on morphometric analyses of the shells and demonstrates that the number of diagnosable species is much higher than 20th century revisions have suggested. On the other hand, several nominal species attributed to *Belgrandia* turned out to belong to *Bythinella* Moquin-Tandon, 1856. I recognize 16 species and one subspecies – this figure does not include Italian taxa, which are the subject of a revision by Italian colleagues – as belonging to *Belgrandia*. The range of this genus covers the Iberian Peninsula, France, Italy, Croatia, and Greece. The highest diversity is found in southern France, with nine species.

Morphologically, the new species is characterized by the combination of a pointed apex, convex whorls, a single varix on the body whorl, which is mostly close to the aperture but may lie up to half a whorl behind it, and a ratio of shell height to shell width of 1.78 (mean). Anatomically diagnostic features are the wide visceral oviduct and the penis, with a wide, rounded muscular lobe on the left side in the distal half. Occasionally, there is a second, smaller lobe on the right side of the penis. The generic allocation is justified through the shell varix and the distal female genitalia with two receptacula seminis and a bursa copulatrix originating from the renal oviduct, which describes a loop of 270°. All specimens investigated anatomically had peritrich ciliates of the genus *Trichodina* Ehrenberg, 1830, in their mantle cavities.

The new species is only known from a single locality. It lives in constantly cool water (11.3–12.3°C), which has high concentrations of calcium and magnesium. However, the concentrations of nitrate, chloride and potassium are also considerable. The sources of this contamination are probably the nearby settlements and agriculture.

Key words: anatomy, *Belgrandia*, Hydrobiidae, morphology, systematics.

## INTRODUCTION

The Petite Camargue Alsacienne is a remnant of the former wetlands on the left bank of the river Rhine about 5 km north of Basel in the southeast of Alsace, France (Fig. 1). These wetlands have been largely destroyed through the construction of two channels, the Canal de Huningue and the Grand Canal d'Alsace, and of embankments during the 19th and early 20th centuries. These measures cut off the wetlands from the Rhine. Regular flooding was prevented, and the groundwater level dropped. But the Petite Camargue Alsacienne partly kept its character as wetland owing to a number of springs emerging in the southwest and water diverted from the Canal de Huningue (Schenker, 1992). The Petite Camargue Alsacienne is characterized by a high diversity of habitats and hence plants and animals and therefore has been declared nature reserve in 1982. Since then, measures for the revitalisation and management have been taken, and an inventory of flora and fauna is being made (Schenker, 1992; Durrer, 1998).

During pilot studies for the inventory of mollusks an hitherto undescribed hydrobiid species belonging to the genus *Belgrandia* Bourguignat, 1869, was found. This genus has been established for species with conical shells bearing one or more varices close to the aperture (Bourguignat, 1869). Later, few anatomical observations also of populations attributed to the type species, *B. gibba* (Draparnaud, 1805), allowed the diagnosis to be extended (Giusti & Pezzoli, 1980). However, comprehensive anatomical studies of representatives of this genus are still scarce, so that it is still not well defined. And

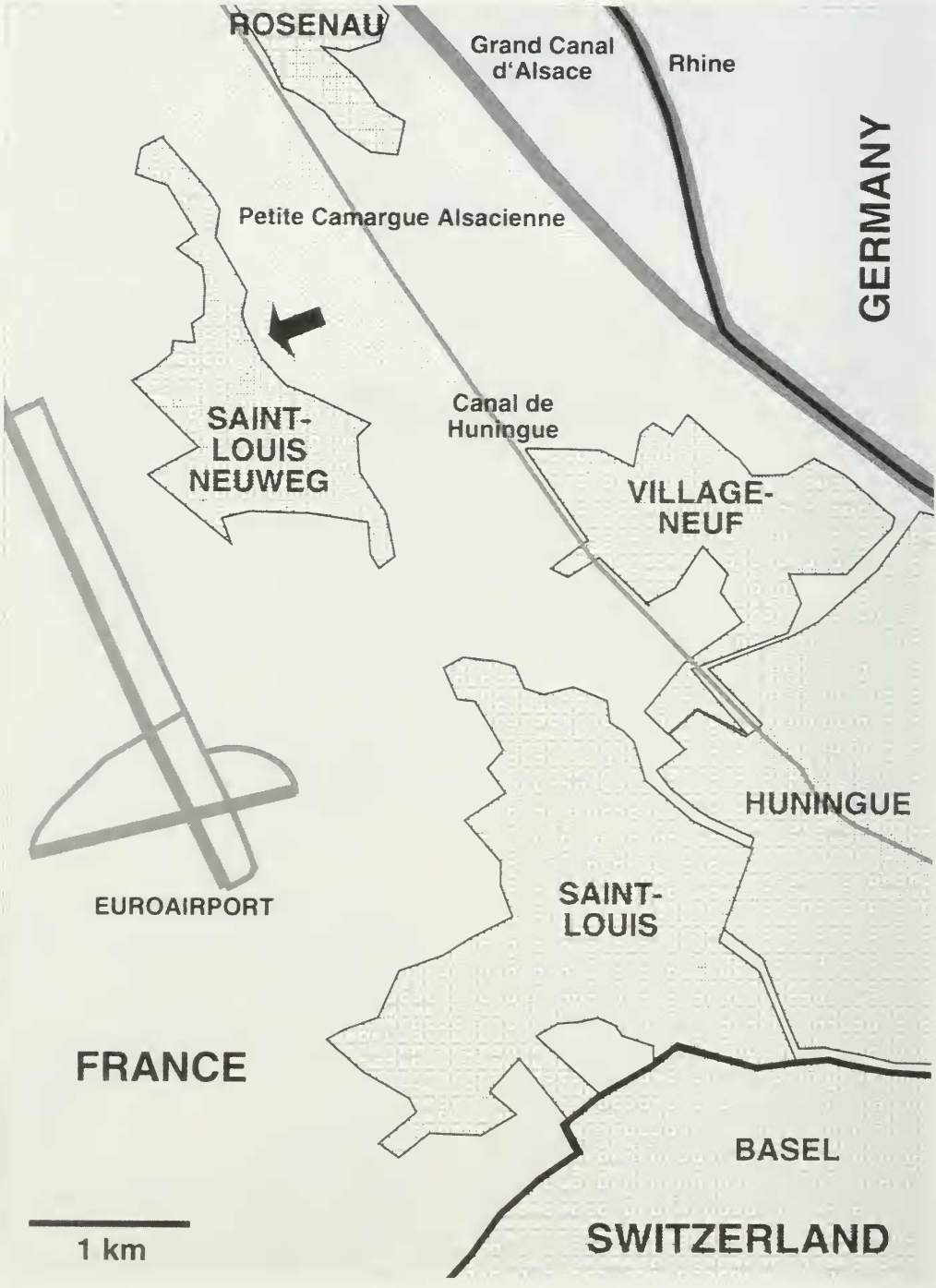


FIG. 1. Situation of the Petite Camargue Alsacienne (stippled area). Arrow indicates type locality of *Belgrandia gfrast*, nov. sp.

the varix is not an apomorphy restricted to *Belgrandia*. It is also found in representatives of the genus *Bythinella* Moquin-Tandon, 1856 (Boeters, 1998; see Discussion).

The Recent distribution of *Belgrandia* ranges from the Iberian Peninsula (Boeters, 1988) over southern and central France (Germain, 1931) to Italy (Giusti & Pezzoli, 1980), Croatia (Schütt, 1961), and Greece (Bodon et al., 1999). Fossil shells attributed to *Belgrandia* were found near Paris (Bourguignat, 1869), in Great Britain (Sandberger, 1880), eastern Germany (Sandberger, 1870–1875), and Latium, Italy (Settepassi & Verdel, 1965).

In order to delimitate the new species, it has been necessary to reinvestigate type material of nominal species at one or another time attributed to *Belgrandia* (Appendix 1). The resulting revision is based only on shell morphology. Therefore, because of the lack of anatomical data, no definite statements can be made about the true generic allocation of species retained in *Belgrandia* and about potential synonymies. On the other hand, it has been possible to exclude and reallocate a number of nominal species. In some cases, the original material could not be traced, or the respective collections were not accessible because of shortage of personnel. In these cases, topotypes were investigated or, where not available, I had to rely on the original descriptions. The species known from Italy are not explicitly treated in the present paper, because they are subject of a revision prepared by Cianfanelli, Bodon, Manganelli & Giusti (pers. comm.). However, I have also investigated the syntypes or topotypes of most of these species for the delimitation of the new species. For this purpose, published, mostly qualitative characters proved to be sufficient, so that new observations on these Italian taxa need not be incorporated in the present account. The same holds for the comparison with *Litthabitella chilodia ionica* Schütt, 1980, recently tentatively attributed to *Belgrandia* (Bodon et al., 1999), which was not available for investigation.

The detailed description of the new species is based on character sets and state definitions provided by Hershler & Ponder (1998), who attempt to standardize the terminology and interpretation of characters used in taxonomic descriptions of hydrobioid gastropods (*sensu* Davis, 1979) as a basis for a phylogenetic analysis of this poorly understood group. In addition, data of ten physicochemical parameters measured in the type locality of the new species by Berger (1993) are provided in order to characterize its habitat in terms of abiotic factors.

## MATERIAL & METHODS

More than 100 specimens of the new species were collected on July 6th, 1998, in the origin of the Chenal des Sources (spring channel) in the Petite Camargue Alsacienne (Fig. 1). The animals were fixed either in 70% ethanol or Bouin's solution. Some of the snails were relaxed with menthol prior to fixation. Shells were measured using a dissecting microscope equipped with an ocular micrometer. The number of whorls was estimated to the nearest eighth of a whorl. Morphometric analyses of nine shell parameters were performed using the computer programs SYNTAX 5.02 (Podani, 1993) and StatView 5.0 (SAS Institute Inc., 1998). Principal component analyses (PCA) were performed starting from correlation matrices. Dendrograms (UPGMA, unweighted pairgroup method using arithmetic averaging; MST, minimum spanning tree) are based on Euclidean distances computed from z-standardized means or individual values where only a single specimen was available. The anatomy was investigated by dissection and reconstruction of histological serial sections using the computer program SURFdriver versions 2.5.5 and 3.0 (Moody & Lozanoff, 1997). The hardparts, which were cleaned with sodium hypochlorite, as well as external features of the critical-point-dried soft body were sputtered with platinum and examined with a Jeol JSM 6300F scanning electron microscope (SEM). The physicochemical data of the origin of the spring channel, the type locality of the new species, presented following the systematic description are taken from Berger (1993), who measured ten parameters from March to December 1990 in weekly intervals.

Abbreviations of museum collections:

BOE, private collection of H. D. Boeters, Munich; GNM, Göteborgs Naturhistoriska Museum (Gothenburg); MHNG, Museum d'Histoire Naturelle (Bourguignat collection), Genève (Geneva); MNHN, Museum National d'Histoire Naturelle, Paris; NHMW, Naturhistorisches Museum Wien (Vienna); NMB, Naturhistorisches Museum Basel; SMF, Naturmuseum und Forschungsanstalt Sencken-

berg, Frankfurt; ZSM, Zoologische Staatssammlung München (Munich).

## RESULTS

### The Species of *Belgrandia*

As mentioned in the Introduction, several old collections are currently not accessible. This holds also for Paladilhe's collection, which is housed in the Medical Faculty of the University of Montpellier. However, Paladilhe extensively exchanged material with Bourguignat, so that many samples of Paladilhe's original material, often syntypes, can be found in Geneva, where Bourguignat's collection has been deposited.

In the following short descriptions, a section Material Examined is inserted in cases where the original material was not available or if a specification is necessary because only part of the type material was investigated. The Descriptions are based on the material examined unless otherwise stated. Additional information from the literature may be given in the Remarks. Lectotypes are designated in order to unambiguously define the respective species. The morphometric data are summarized in Table 1. I do not refer to this table each time. Only those parameters characterizing a species are mentioned. The power of the statistical tests is quite low in most cases, for which only a small number of individuals was available. Therefore, the Bonferroni procedure correcting $\alpha$ in multiple parallel tests has to be considered conservative. The Remarks discuss only species-specific, taxonomic issues. Other issues are put into a wider context in the Discussion.

#### *Belgrandia*
Bourguignat, 1869

*Belgrandia* Bourguignat, 1869: 13–15

*Thermhydrobia* Paulucci, 1878 – Clessin, 1882: 137 f.

*Type Species: Cyclostoma gibbum* Draparnaud, 1805, by subsequent designation (Kobelt, 1878).

*Diagnosis:* Shell conical, with pointed apex; one or several varices on the body whorl, occasionally there is no varix or it is replaced by folds; aperture oval; ctenidium with about ten filaments; radula with a single pair of basal cusps on the central tooth; penis with one muscular lobe on the left side, occasionally a second lobe on the right side; female genital system with a sac-shaped bursa copulatrix and two seminal receptacles, the proximal one arising from the proximal-most point of the loop of the renal oviduct, the distal one shortly before the origin of the bursal duct; renal oviduct unpigmented, describing a simple, wide loop of 270°.

*Remarks:* This diagnosis is largely based on the findings of Giusti & Pezzoli (1980). As already mentioned before, only few (nominal) species have been investigated anatomically, so that this diagnosis has to be considered preliminary and will probably be extended when more data become available. At present the following characters allow to differentiate species: shell shape; number, position, and formation of varices; shape of penis; number, position, and formation of penial lobes.

#### *Belgrandia gibba*
(Draparnaud, 1805)

*Cyclostoma gibbum* Draparnaud, 1805: 38

*Belgrandia varica* (Paget, 1854) – Germain, 1913: 301

*Belgrandia moitessieri* (Bourguignat, 1866) – Germain, 1913: 301

*Belgrandia gibberula* Paladilhe, 1869 – Germain, 1913: 301

*Belgrandia cazioti* Locard, 1892 – Germain, 1913: 301

*Hydrobia paladilhi* Moitessier, 1869 – Germain, 1931: 632

*Belgrandia bourguignati* de Saint-Simon, 1870 – Germain, 1931: 632

*Type Material:* lectotype NHMW 100519, here designated in order to define the species; paralectotypes NHMW 100520 (3)

*Type Locality:* France, not further specified

*Description:* Shell (Fig. 2A) high (mean 2.13 mm), moderately slender, with up to 4.375 whorls; deep sutures separate the markedly convex whorls; up to five very prominent varices on body whorl up to 1/2 a whorl behind outer lip; aperture small relative to shell; umbilicus very narrow.

*Remarks:* The precise origin of Draparnaud's specimens is not known. Draparnaud lived in Montpellier, and therefore it is usually assumed that the species he described were collected in southern France. Giusti & Pezzoli (1980) investigated individuals from two

French populations they attributed to *B. gibba* and described the penis as being conical and pointed, with a short, pointed lobe on the left side close to the tip.

The synonymization of six nominal species with *B. gibba* by Germain (1913, 1931) is problematical, because he did not give arguments. The only feature all these species have in common is their occurrence in southern France. However, the morphometric analysis (Figs. 4, 5; Appendix 2) indicates that probably none of them is *B. gibba,* and most of them may be good species. This issue is further discussed for each nominal species under its respective description.

Moquin-Tandon (1856) has introduced the three varieties *uniplicata, marginata* and *aplexa,* which differ only in the number and position of the varices. Taxonomically, this differentiation is certainly not warranted, since all three varieties are from a single locality, the source of the river Lez near Montpellier. To which species these varieties really belong could not be determined, because the whereabouts of Moquin-Tandon's syntypes are not known. Therefore, I tentatively consider all three varieties as synonyms of *B. gibba.*

### *Belgrandia marginata* (Michaud, 1831)

*Paludina marginata* Michaud, 1831: 98

*Belgrandia boscae* Salvana (1877)—Boeters, 1988: 223

*Type Material:* not traced

*Type Locality:* Draguignan, river Var, France

*Material Examined:* Foux de Draguignan, France, ex BOE 291a (10)

*Description:* Shell (Fig. 2B) very slender, on average 1.83 mm high and thus rather small, with slightly more than four markedly convex whorls; spire high relative to aperture height; aperture almost as high as wide with a straight outer lip (frontal view); one prominent varix close to lip; umbilicus a very narrow slit.

*Remarks: Belgrandia boscae* should not be regarded as synonym for reasons outlined below.

### *Belgrandia conoidea* (Reynies, 1844)

*Paludina conoidea* Reynies, 1844: 4 f.

*Type Material:* not traced

*Type Locality:* Ardus sur l'Aveyron, near Montauban, France

*Material Examined:* Le Lez à Montpellier MHNG (2)

*Description:* Shell (Fig. 2C) broadly conical, high (larger specimen 2.14 mm), with about four convex whorls; aperture high relative to shell height; body whorl without varices; umbilicus a more or less narrow slit.

*Remarks:* This species has been largely neglected in 20th century revisions of the French malacofauna. Recently, it has been attributed to *Belgrandia* (Falkner et al., in prep.). However, since this species lacks varices, this allocation must remain doubtful until confirmation through anatomical investigations. It is of course possible that *B. conoidea* has lost the varices and hence this state is apomorphic. Reynies' syntypes could not be traced. The material examined from Bourguignat's collection is probably a sample mentioned and attributed to this species, albeit under the genus *Hydrobia* Hartmann, 1821, by Paladilhe (1870). Thus, it is questionable that this sample really belongs to *B. conoidea.*

### *Belgrandia varica* (Paget, 1854)

*Hydrobia varica* Paget 1854: 454 f.

*Belgrandia gibba* (Draparnaud, 1805)—Germain, 1913: 301

*Type Material:* not traced

*Type Locality:* river Var near Nizza below the mill of Davigo and a ditch at the Grenouillères

*Description:* Shell ovate-conical, up to 2 mm high and 1.25 mm wide with up to 4 whorls, which are separated by deep sutures; last whorl ventricose, not detached, a single varix close to outer lip; aperture oblique, with an obtuse angle.

*Remarks:* This description is based on Paget's (1854) original. His collection is apparently lost. Although Paget quite clearly distinguished his species from *B. gibba,* and although the type localities of these species are distant from each other, Germain (1913) considered *B. varica* as junior synonym of the latter. Considering the type locality of *B. varica,* one might rather assume affinities with *B. marginata.* Both hypotheses, however, would need verification through the investigation of topotypical material, which requires that the type locality is still intact.

TABLE 1. Shell measurements. Ab, abbreviation; ah, aperture height; aw, aperture width; cv, coefficient of variation [corrected for sample size following Sokal & Rohlf (1995)]; max, maximum; min, minimum; s, standard deviation; sh, shell height; sw, shell width; W, number of whorls; x, mean.

| Species | Status | Ab | | sh | sw | ah | aw | W | sh/sw | ah/aw | sh/ah | sw/aw |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *B. bigorriensis* | lectotype | B | | 2.44 | 1.30 | 0.89 | 0.76 | 4.625 | 1.87 | 1.16 | 2.75 | 1.71 |
| *B. boscae* | topotypes | E | min | 1.68 | 0.90 | 0.66 | 0.60 | 3.500 | 1.66 | 1.10 | 2.40 | 1.50 |
| N = 5 | | | max | 2.00 | 1.06 | 0.79 | 0.65 | 4.000 | 1.98 | 1.27 | 2.57 | 1.77 |
| | | | x | 1.83 | 0.98 | 0.73 | 0.61 | 3.78 | 1.86 | 1.19 | 2.49 | 1.59 |
| | | | s | 0.13 | 0.06 | 0.05 | 0.02 | 0.21 | 0.13 | 0.07 | 0.08 | 0.11 |
| | | | cv | 7.16 | 6.47 | 6.76 | 3.48 | 5.71 | 7.18 | 5.80 | 3.34 | 7.43 |
| *B. cazioti* Westerlund | lectotype | W | | 2.02 | 1.35 | 0.86 | 0.74 | 3.875 | 1.50 | 1.16 | 2.35 | 1.82 |
| *B. cazioti* Locard | syntypes | Z | min | 2.02 | 1.06 | 0.77 | 0.68 | 4.125 | 1.81 | 1.07 | 2.59 | 1.56 |
| N = 5 | | | max | 2.30 | 1.26 | 0.88 | 0.78 | 4.250 | 1.92 | 1.13 | 2.81 | 1.62 |
| | | | x | 2.19 | 1.17 | 0.81 | 0.73 | 4.200 | 1.87 | 1.11 | 2.70 | 1.60 |
| | | | s | 0.11 | 0.08 | 0.04 | 0.04 | 0.07 | 0.05 | 0.03 | 0.09 | 0.02 |
| | | | cv | 5.46 | 6.78 | 5.44 | 4.60 | 1.71 | 2.59 | 2.57 | 3.44 | 1.43 |
| *B. conoidea* | | D | min | 2.10 | 1.20 | 0.82 | 0.70 | 4.000 | 1.64 | 1.16 | 2.44 | 1.69 |
| N = 2 | | | max | 2.14 | 1.28 | 0.86 | 0.71 | 4.000 | 1.78 | 1.23 | 2.61 | 1.83 |
| | | | x | 2.12 | 1.24 | 0.84 | 0.71 | 4.000 | 1.71 | 1.19 | 2.53 | 1.76 |
| | | | s | 0.03 | 0.06 | 0.03 | 0.01 | 0 | 0.10 | 0.05 | 0.12 | 0.10 |
| | | | cv | 1.50 | 5.13 | 3.79 | 1.13 | 0 | 6.63 | 4.92 | 5.29 | 6.26 |
| *B. coutagnei* | syntypes | K | min | 2.14 | 1.04 | 0.77 | 0.64 | 4.250 | 1.99 | 1.08 | 2.74 | 1.57 |
| N = 4 | | | max | 2.51 | 1.26 | 0.86 | 0.78 | 5.000 | 2.07 | 1.27 | 2.99 | 1.77 |
| | | | x | 2.33 | 1.15 | 0.81 | 0.70 | 4.59 | 2.03 | 1.17 | 2.87 | 1.64 |
| | | | s | 0.19 | 0.10 | 0.04 | 0.06 | 0.31 | 0.04 | 0.09 | 0.10 | 0.08 |
| | | | cv | 8.64 | 9.12 | 5.77 | 8.94 | 7.23 | 2.02 | 8.29 | 3.72 | 5.41 |
| | lectotype | | | 2.51 | 1.26 | 0.84 | 0.78 | 4.625 | 1.99 | 1.08 | 2.99 | 1.62 |
| *B. gfrast* females | holotype + 14 | F | min | 2.02 | 1.14 | 0.78 | 0.68 | 3.750 | 1.57 | 1.11 | 2.24 | 1.58 |
| N = 15 | paratypes | | max | 2.34 | 1.29 | 0.92 | 0.79 | 4.375 | 1.95 | 1.21 | 2.75 | 1.81 |
| | | | x | 2.16 | 1.22 | 0.86 | 0.73 | 4.000 | 1.78 | 1.18 | 2.51 | 1.66 |
| | | | s | 0.10 | 0.05 | 0.05 | 0.03 | 0.16 | 0.10 | 0.03 | 0.12 | 0.06 |
| | | | cv | 4.53 | 3.80 | 5.37 | 4.65 | 4.16 | 5.72 | 2.74 | 4.93 | 3.70 |
| | holotype | | | 2.34 | 1.20 | 0.85 | 0.70 | 4.375 | 1.95 | 1.21 | 2.75 | 1.71 |
| *B. gibba* | syntypes | G | min | 2.08 | 1.06 | 0.74 | 0.62 | 4.000 | 1.74 | 1.11 | 2.67 | 1.58 |
| N = 4 | | | max | 2.16 | 1.24 | 0.78 | 0.67 | 4.375 | 2.02 | 1.26 | 2.89 | 1.88 |
| | | | x | 2.12 | 1.14 | 0.77 | 0.65 | 4.13 | 1.87 | 1.18 | 2.78 | 1.76 |
| | | | s | 0.03 | 0.08 | 0.02 | 0.02 | 0.18 | 0.12 | 0.07 | 0.11 | 0.14 |
| | | | cv | 1.71 | 7.25 | 2.66 | 3.64 | 4.55 | 6.98 | 6.15 | 4.01 | 8.29 |
| | lectotype | | | 2.16 | 1.24 | 0.76 | 0.66 | 4.125 | 1.74 | 1.15 | 2.84 | 1.88 |
| *B. gibberula* | syntypes | I | min | 1.68 | 1.10 | 0.77 | 0.69 | 3.250 | 1.52 | 1.08 | 2.17 | 1.54 |
| Source de Verdua | | | max | 2.04 | 1.25 | 0.88 | 0.79 | 3.750 | 1.70 | 1.18 | 2.43 | 1.64 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| N = 15 | | | x | 1.89 | 1.16 | 0.82 | 0.73 | 3.54 | 1.63 | 1.12 | 2.31 | 1.59 |
| | | | s | 0.09 | 0.05 | 0.04 | 0.03 | 0.15 | 0.07 | 0.03 | 0.09 | 0.03 |
| | | | cv | 4.94 | 4.15 | 4.58 | 4.56 | 4.22 | 4.26 | 2.61 | 3.81 | 1.94 |
| | lectotype | | | 1.99 | 1.14 | 0.82 | 0.72 | 3.750 | 1.75 | 1.14 | 2.43 | 1.58 |
| *B. gibberula* | | H | min | 1.93 | 1.07 | 0.76 | 0.64 | 3.750 | 1.66 | 1.09 | 2.33 | 1.60 |
| Herault | | | max | 2.29 | 1.27 | 0.84 | 0.76 | 4.250 | 1.94 | 1.27 | 2.73 | 1.76 |
| N = 5 | | | x | 2.06 | 1.16 | 0.80 | 0.69 | 3.98 | 1.79 | 1.17 | 2.58 | 1.69 |
| | | | s | 0.14 | 0.07 | 0.04 | 0.05 | 0.19 | 0.11 | 0.08 | 0.17 | 0.06 |
| | | | cv | 7.20 | 6.69 | 4.91 | 7.15 | 4.90 | 6.71 | 6.99 | 6.98 | 3.81 |
| *B. gibberula* var. | | V | min | 1.88 | 1.06 | 0.73 | 0.64 | 3.500 | 1.70 | 1.09 | 2.43 | 1.58 |
| N = 15 | | | max | 2.24 | 1.19 | 0.85 | 0.74 | 4.000 | 1.90 | 1.22 | 2.62 | 1.73 |
| St. Jean de Fos | | | x | 1.98 | 1.11 | 0.78 | 0.68 | 3.78 | 1.78 | 1.15 | 2.54 | 1.64 |
| | | | s | 0.10 | 0.04 | 0.04 | 0.03 | 0.14 | 0.05 | 0.04 | 0.07 | 0.04 |
| | | | cv | 5.20 | 3.37 | 4.52 | 4.36 | 3.69 | 2.96 | 3.31 | 2.84 | 2.56 |
| *B. heussi heussi* | paratypes | U | min | 1.81 | 0.97 | 0.68 | 0.57 | 4.250 | 1.85 | 1.15 | 2.66 | 1.66 |
| N = 2 | | | max | 1.86 | 0.98 | 0.69 | 0.59 | 4.250 | 1.92 | 1.21 | 2.70 | 1.70 |
| | | | x | 1.84 | 0.98 | 0.69 | 0.58 | 4.250 | 1.88 | 1.18 | 2.69 | 1.68 |
| | | | s | 0.04 | 0.01 | 0.01 | 0.01 | 0 | 0.05 | 0.04 | 0.02 | 0.03 |
| | | | cv | 2.17 | 0.82 | 1.16 | 2.74 | 0 | 2.98 | 3.90 | 1.01 | 1.93 |
| *B. h. alcoaensis* | paratype | A | | 1.90 | 1.10 | 0.76 | 0.65 | 4.000 | 1.73 | 1.17 | 2.50 | 1.69 |
| *B. lusitanica* | syntypes | L | min | 1.60 | 0.86 | 0.58 | 0.52 | 3.750 | 1.78 | 1.07 | 2.49 | 1.59 |
| N = 6 | | | max | 1.82 | 0.92 | 0.66 | 0.58 | 4.500 | 1.98 | 1.23 | 2.84 | 1.73 |
| | | | x | 1.69 | 0.90 | 0.62 | 0.55 | 4.06 | 1.89 | 1.14 | 2.72 | 1.64 |
| | | | s | 0.09 | 0.03 | 0.04 | 0.03 | 0.25 | 0.08 | 0.05 | 0.14 | 0.05 |
| | | | cv | 5.37 | 3.15 | 5.76 | 4.87 | 6.33 | 4.55 | 4.75 | 5.32 | 3.22 |
| | lectotype | | | 1.82 | 0.92 | 0.64 | 0.57 | 4.500 | 1.98 | 1.13 | 2.85 | 1.61 |
| *B. marginata* | topotypes | M | min | 1.70 | 0.88 | 0.61 | 0.55 | 3.750 | 1.79 | 1.00 | 2.62 | 1.39 |
| N = 10 | | | max | 2.05 | 0.98 | 0.70 | 0.70 | 4.500 | 2.16 | 1.16 | 3.04 | 1.66 |
| | | | x | 1.83 | 0.94 | 0.66 | 0.60 | 4.03 | 1.95 | 1.10 | 2.78 | 1.57 |
| | | | s | 0.11 | 0.03 | 0.03 | 0.04 | 0.24 | 0.10 | 0.05 | 0.12 | 0.07 |
| | | | cv | 6.08 | 3.41 | 4.53 | 7.21 | 6.13 | 5.40 | 4.89 | 4.47 | 4.84 |
| *B. moitessieri* | syntypes | T | min | 1.57 | 0.94 | 0.62 | 0.58 | 3.250 | 1.58 | 0.97 | 2.26 | 1.47 |
| N = 10 | | | max | 1.84 | 1.05 | 0.74 | 0.66 | 3.750 | 1.76 | 1.13 | 2.69 | 1.70 |
| | | | x | 1.68 | 0.99 | 0.67 | 0.62 | 3.53 | 1.69 | 1.08 | 2.52 | 1.61 |
| | | | s | 0.09 | 0.03 | 0.04 | 0.03 | 0.21 | 0.06 | 0.05 | 0.12 | 0.07 |
| | | | cv | 5.58 | 3.30 | 5.81 | 4.96 | 6.13 | 3.44 | 4.65 | 4.84 | 4.41 |
| | lectotype | | | 1.73 | 1.02 | 0.70 | 0.63 | 3.500 | 1.70 | 1.11 | 2.47 | 1.62 |
| *B. torifera* | topotypes | Y | min | 1.56 | 0.96 | 0.68 | 0.62 | 3.625 | 1.55 | 1.00 | 2.25 | 1.46 |
| N = 5 | | | max | 1.70 | 1.10 | 0.74 | 0.74 | 3.875 | 1.63 | 1.11 | 2.32 | 1.65 |
| | | | x | 1.64 | 1.03 | 0.71 | 0.67 | 3.75 | 1.58 | 1.07 | 2.29 | 1.54 |
| | | | s | 0.06 | 0.06 | 0.03 | 0.06 | 0.09 | 0.03 | 0.05 | 0.03 | 0.07 |
| | | | cv | 4.00 | 5.73 | 4.11 | 8.52 | 2.48 | 2.07 | 4.91 | 1.16 | 4.58 |


FIG. 2. Shells. A, *B. gibba,* lectotype (left) and 2 paralectotypes; B, *B. marginata,* topotypes; C, *B. conoidea,* D, *B. moitessieri,* lectotype (left) and 2 paralectotypes; E, *B. gibberula,* lectotype (left) and 2 paralectotypes; F, *B. gibberula* var.; G, *B. gfrast,* nov. sp., 3 paratypes. Scale bar = 2 mm.

*Belgrandia moitessieri*
(Bourguignat, 1866)

*Hydrobia moitessieri* Bourguignat, 1866: 191

*Belgrandia gibba* (Draparnaud, 1805)—Germain, 1913: 301

*Type Material:* lectotype MHNG, here designated in order to define the species; paralectotypes MHNG (11)

*Type Locality:* source of the river Martinet near Montpellier, France

*Description:* Shell (Fig. 2D) broadly conical, with a height of on average 1.68 mm very

small, up to 3.75 rapidly growing, convex whorls; body whorl inflated; almost round aperture wide relative to shell width; 0–3 varices not more than 1/4 whorl behind the outer lip; umbilicus a narrow slit.

*Remarks:* This species can readily be distinguished from *B. gibba* in all parameters measured but aperture width and the ratio shell width/aperture width (Mann Whitney U-test, $P < 0.05$; however, after Bonferroni-correction the three other ratios are also no longer significant), and is very remote from all other species in the morphospace displayed by the PCA in Fig. 5 (for details about the PCA, see Appendix 2). Consequently, *B. moitessieri* should be treated as a valid species until anatomical data might prove the contrary.

### *Belgrandia lusitanica* (Paladilhe, 1867)

*Paludina gibba* (Michaud, 1831)—Morelet, 1845: 91

*Hydrobia lusitanica* Paladilhe, 1867: 60 f

*Belgrandia occidentalis* Clessin, 1878—Clessin, 1882: 136

*Hydrobia gibba* (Draparnaud, 1805)—Nobre, 1885: 58

*Type Material:* lectotype [MHNG], here designated in order to define the species; paralectotypes [MHNG (5)]

*Type Locality:* Fonte das Lagrimas near Coimbra, Portugal

*Description:* Shell (Fig. 3E) slender conical, small, with a height of on average 1.69 mm; slightly more than four not very convex whorls; aperture adapically with a more or less distinct angle; one distinct varix closely behind outer lip; umbilicus a very narrow slit; some individuals carry egg capsules mainly on sutures.

*Remarks: Belgrandia lusitanica* cannot be confused with *B. gibba,* because it is much smaller and has constantly a single varix behind the outer lip, contrary to *B. gibba,* where up to five varices which are, in addition, much more prominent, can be found. Clessin (1878a) overlooked Paladilhe's description when he introduced *B. occidentalis* and subsequently put his own name in synonymy (Clessin, 1882). Very similar and geographically closest is *B. heussi heussi* Boettger, 1963 (Fig. 5). The differentiation of these species is discussed in the Remarks to the latter.

### *Belgrandia bigorriensis* Paladilhe, 1869

*Belgrandia bigorriensis* Paladilhe, 1869: 125 f

*Belgrandia vitrea* (Draparnaud, 1801)—Germain, 1913: 303

*Type Material:* lectotype MHNG, here designated in order to define the species; paralectotype MHNG (1)

*Type Locality:* a ferruginous spring near Bigorre, France

*Description:* Conical shell (Fig. 3A) relatively large, with a height of 2.44 mm; the lectotype has 4.625 convex whorls; aperture narrow relative to shell width; one not very prominent varix close to outer lip; umbilicus an open slit.

*Remarks:* Only the lectotype could be investigated, because the paralectotype once had apparently been glued onto cardboard and still has remnants of the glue. According to Paladilhe's (1969) original description, there can be a second varix. The most similar species is *B. coutagnei* Locard, 1892. However, this species is smaller, more slender and has a much wider aperture relative to shell size. *Belgrandia bigorriensis* is clearly a distinct species.

*Belgrandia vitrea* (*Cyclostoma vitreum*) has been identified as belonging to *Moitessieria* Bourguignat, 863 (Boeters, 1969, 1972), which is conchologically characterized by a very slender, turriform shell with fine spiral sculpture. Therefore, *B. bigorriensis* cannot be a junior synonym of Draparnaud's species.

### *Belgrandia gibberula* Paladilhe, 1869

*Belgrandia gibberula* Paladilhe, 1869: 126–128

*Hydrobia paladilhi* Dubrueil, 1869—Paladilhe, 1870: 228

*Belgrandia gibba* (Draparnaud, 1805)—Germain, 1913: 301

*Type Material:* lectotype MHNG, here designated in order to define the species; paralectotypes MHNG (>50)

*Type Locality:* Source de Verdun near Saint Guilhem-le-Désert, France

*Description:* Shell (Fig. 2E) on average 1.89 mm high, ovate conical; mean number of whorls (3.54), which are convex and slightly shouldered, low; aperture in both directions measured wide relative to shell size; 0–2

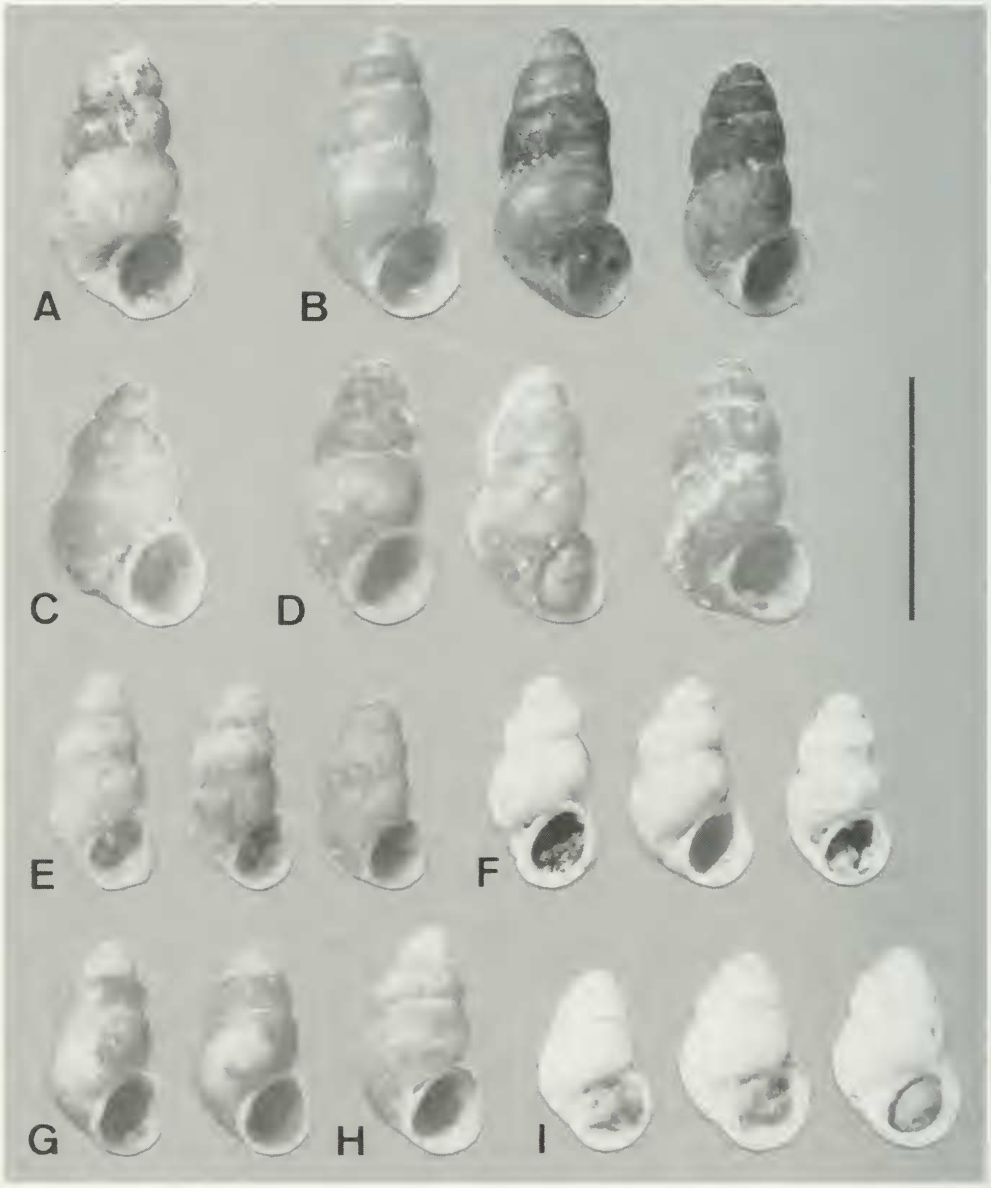


FIG. 3. Shells. A, *B. bigorriensis,* lectotype; B, *B. coutagnei,* lectotype (left) and 2 paralectotypes; C, *B. cazioti* Westerlund, lectotype; D, *B. cazioti* Locard non Westerlund, syntypes; E, *B. lusitanica,* lectotype (left) and 2 paralectotypes; F, *B. boscae*, topotypes; G, *B. heussi heussi,* paratypes; H, *B. heussi alcoaensis,* paratype; I, *B. torifera,* topotypes. Scale bar = 2 mm.

rather flat varices on the last 0.25 whorls; umbilicus a very narrow slit or completely covered.

*Remarks: Belgrandia gibberula* is morphometrically unique (Figs. 4, 5) and can hardly be confused with any other species. That holds also for a comparison with *B. gibba,* which is larger, more slender, has a smaller aperture, non-shouldered whorls, and up to five very prominent varices. Therefore, a synonymization of both species is unwarranted.

Paladilhe (1870) considered *Hydrobia pal-*

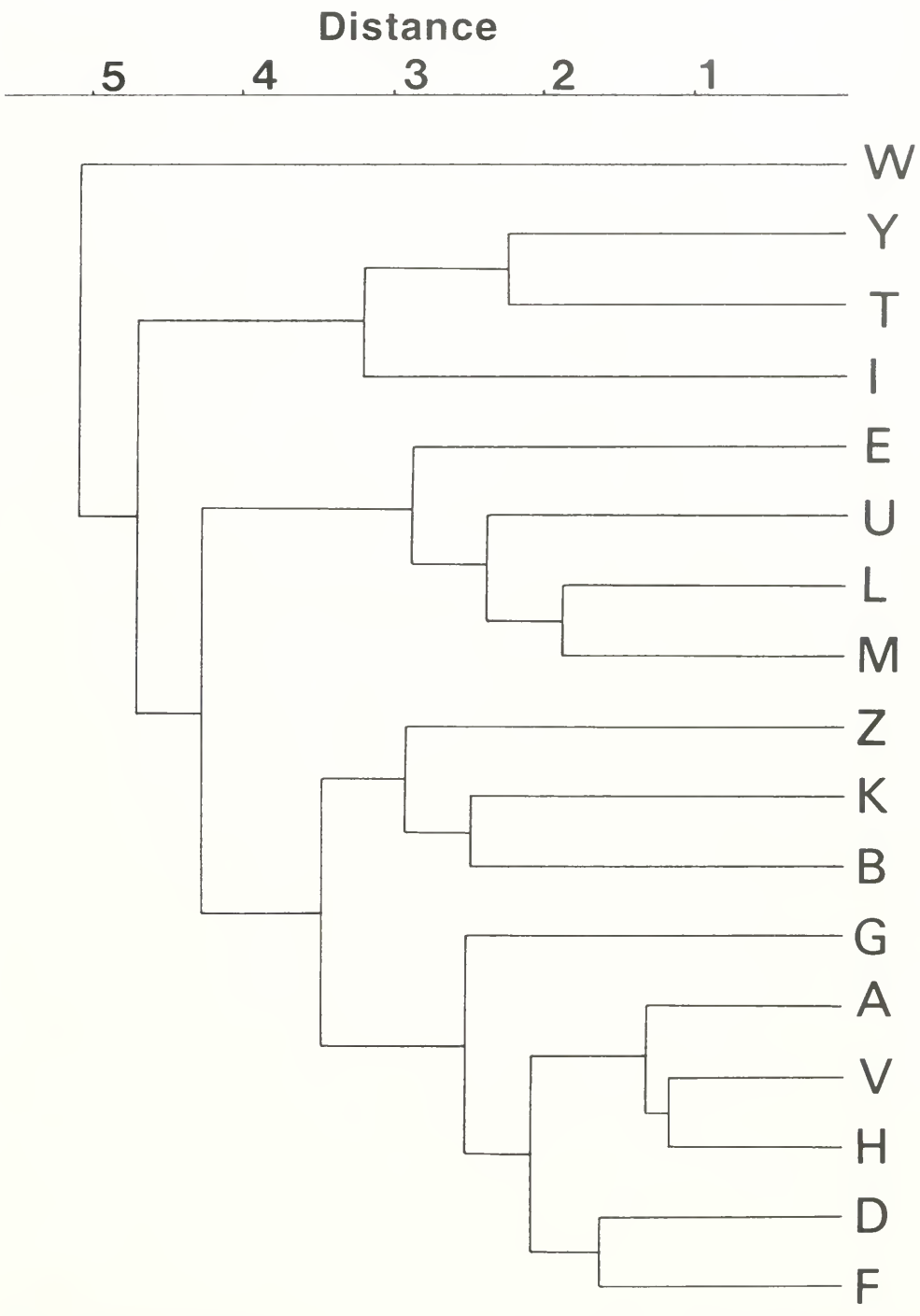


FIG. 4. UPGMA dendrogram based on z-standardized Euclidean distances computed from the nine shell parameters of Table 1. For abbreviations of populations, see Table 1.

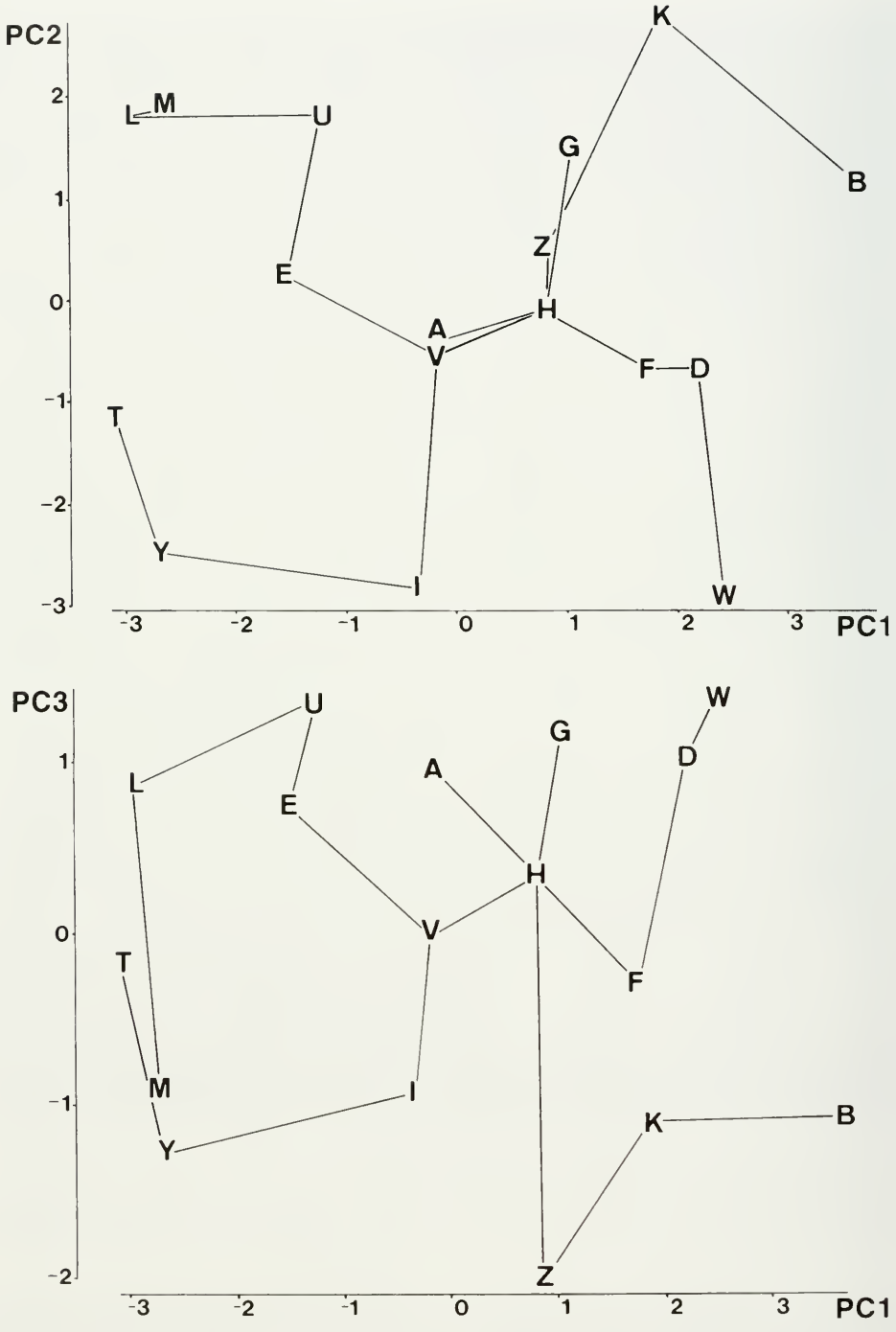


FIG. 5. Minimum spanning tree based on z-standardized Euclidean distances computed from the nine shell parameters of Table 1 superimposed on ordinations following a principal component analysis of these parameters. For abbreviations of populations, see Table 1; PC, principal component.

*adilhi* Dubrueil, 1869 [Germain (1931: 632) erroneously attributed the authorship of this taxon to Moitessier, 1869], as juveniles of *B. gibberula*. Dubrueil's syntypes from Frouzet near St. Martin de Londres, at least a subsample, have been found in Bourguignat's collection (MHNG). This sample consists of five juvenile shells. However, it is impossible to decide whether they represent a good species or belong to an older taxon.

Two more samples from Bourguignat's collection, one labelled as *B. gibberula* Paladilhe, Département Hérault, the other one *B. gibberula* Paladilhe Var. from St. Jean de Fos, Hérault (Fig. 2F), were investigated, primarily in order to get an idea of the variability of *B. gibberula* for comparisons with the new species described below, which is, on a first glance, similar to *B. gibberula*. This comparison is discussed in detail in the Remarks to the new species. In both samples, egg capsules attached to shells were found.

*Belgrandia paladilhi*
(Dubrueil, 1869)

See Remarks to *B. gibberula*.

*Belgrandia occidentalis*
Clessin, 1878

See Remarks to *B. lusitanica*.

*Belgrandia germanica*
Clessin, 1878

*Belgrandia marginata* (Michaud, 1831)—Sandberger, 1870–1875: 915 f.

*Belgrandia germanica* Clessin, 1878b: 101

*Type Material:* not traced

*Type Locality:* upper Pleistocene tuffs of Weimar, Gräfentonna and Mühlhausen, Germany

*Description:* Shell cylindro-conical, up to 2.25 mm high and 1.25 mm wide; apex blunt, up to six convex whorls separated by deep sutures; body whorl almost as high as spire; aperture almost round; a single varix behind outer lip; umbilicus almost completely covered.

*Remarks:* Sandberger's original material is probably lost. Therefore, the above description is a reproduction of the original. Sandberger (1870–1875) identified his fossil species from eastern Germany as *B. marginata*. Hence, Clessin (1878b) introduced the new name *B. germanica* and later differentiated it from *B. marginata* through its shorter and more conical spire (Clessin, 1882).

*Belgrandia boscae*
(Salvana, 1887)

*Hydrobia boscae* Salvana, 1887: 141

*Belgrandia* cf. *marginata* (Michaud, 1831)—Boeters, 1988: 223

*Moitessieria locardi* Coutagne, 1883—Bofill Poch, 1924: 99

*Type Material:* not traced

*Type Locality:* springs at Gandia, Valencia, Spain

*Material Examined:* Gandia, Acequia El Banador, Spain, ex BOE 1455 (5)

*Description:* Shell (Fig. 3F) small (1.83 mm high), moderately slender; up to four convex whorls separated by deep sutures; aperture ovate, peristome slightly reflected; a single, not very prominent varix closely behind outer lip; umbilicus a moderately narrow slit.

*Remarks:* According to Boeters (1988), the varix may be very weak or even absent. Although *B. boscae* is very similar to *B. marginata* as regards shell size and shape, there are some qualitative states that distinguish both taxa, such as the reflected peristome and the less prominent varix in *B. boscae*, or the straight outer lip and the narrower umbilicus in *B. marginata*, so that these nominal species are probably not conspecific. In addition, it is very unlikely that a crenobiontic species has a range from southeastern France across the Pyrenees to western Spain. Therefore, I suggest that *B. boscae* is a distinct species.

*Belgrandia cazioti*
Westerlund, 1890

*Paludinella* (*Belgrandia*) *cazioti* Westerlund, 1890: 154

*Type Material:* lectotype GNM 4417, here designated in order to define the species; paralectotype GNM 4417a (1)

*Type Locality:* Les Angles, France

*Description:* Shell (Fig. 3C) very broadly conical, lectotype 2.02 mm high and 1.35 mm wide; 3.875 very convex and rapidly growing whorls; aperture ovate; lectotype has four very prominent varices on the last 0.25 whorls; umbilicus an open slit.

*Remarks:* The paralectotype is damaged so that measurements could not be taken and the total number of varices not be determined. Through its gross appearance this species cannot be mistaken with any other congeneric species. *Belgrandia cazioti* Locard, 1892, is a different species and thus a junior homonym of *B. cazioti* Westerlund, 1892 (see below).

*Belgrandia cazioti*
Locard, 1892, *non* Westerlund, 1890

*Belgrandia cazioti* Locard, 1892: 3
*Belgrandia gibba* (Draparnaud, 1805)—Germain, 1913: 301
*Type Material:* syntypes MNHN
*Type Locality:* quarter Champfleuri near Avignon, France
*Description:* Shell (Fig. 3D) large, conical, with a mean height of 2.19 mm; on average 4.2 little convex whorls; aperture wide relative to shell width; one prominent varix near but not immediately behind aperture; umbilicus a slit.
*Remarks:* There may be two varices according to the original description (Locard, 1892).
*Belgrandia cazioti* Locard, 1892, is clearly not identical with *B. cazioti* Westerlund, 1890, and, hence, is a junior homonym of the latter. Figures 4 and 5 indicate that it might well be a separate species, with *B. coutagnei* Locard, 1892, as the most similar congeneric. It differs significantly from *B. coutagnei* in number of whorls and the shape indicators shell height/shell width and shell height/aperture height (Mann-Whitney U-test, $P \leq 0.05$). However, after Bonferroni correction, these comparisons are no longer significant. According to Locard (1892), both species are sympatric. It is thus not unlikely that Locard separated the slender and stouter shells of a single population and ascribed them to different taxa. Because of this circumstantial evidence, I suggest to consider *B. cazioti* Locard as synonym of *B. coutagnei*.

*Belgrandia coutagnei*
Locard, 1892

*Belgrandia coutagnei* Locard, 1892: 3
*Belgrandia vitrea* (Draparnaud, 1801)—Germain, 1913: 303
*Belgrandia cazioti* Locard, 1892—present paper
*Type Material:* Lectotype MNHN, here designated in order to define the species; paralectotypes MNHN (3)
*Type Locality:* quarter Champfleuri near Avignon, France
*Description:* Shell (Fig. 3B) large, with an average height of 2.33 mm, slender conical with up to 5 (mean 4.59) convex whorls; aperture ovate, small compared to shell height; one varix immediately behind outer lip; umbilicus a narrow, but distinct slit.
*Remarks:* Locard (1892, 1893) described 1–2 varices in this species. However, all four syntypes have only one. The most similar species is *B. bigorriensis* (Figs. 4, 5). The differentiation of both species is already given in the Remarks to *B. bigorriensis*.
As to the potential synonymy with *B. vitrea,* see Remarks to *B. bigorriensis* Paladilhe, 1869.

*Belgrandia torifera*
Schütt, 1961

*Belgrandia torifera* Schütt, 1961: 143 f.
*Type Material:* holotype SMF 164357; paratypes SMF 164358, private collection of H. Schütt
*Type Locality:* spring Stenjevac near Vrgorac, Croatia
*Material Examined:* topotypes NHMW 16716 (1), NHMW 48796 (5)
*Description:* Shell (Fig. 3I) small (mean 1.64 mm), broadly conical, with on average 3.75 rapidly and regularly growing, convex whorls; aperture practically as wide as high, large relative to shell size; one prominent varix immediately behind outer lip and occasionally a second, weaker one up to 0.75 whorls behind the outer lip; umbilicus almost completely covered.
*Remarks:* Both samples were pooled for the analysis but one shell from the larger lot was excluded because it was very different in size and shape, which may be due to parasitism. In size, *B. torifera* is similar to *B. moitessieri,* but it differs from the latter in its regular growth, the larger aperture and the formation and position of the varices. In general, *B. torifera* is isolated in the morphospace of Figure 5.
This species is the eastern-most representative of the genus and up to now the only one known from the Balkans. Its allocation to *Belgrandia* is of course, as holds for the majority of the species discussed in this paper, tentative and needs confirmation through anatomical data.

*Belgrandia heussi heussi*
Boettger, 1963

*Belgrandia heussi heussi* Boettger, 1963: 40–42

*Type Material:* holotype SMF 167898; paratypes SMF 167898 (18)

*Type Locality:* Rio Liz, Portugal

*Material Examined:* two paratypes ex SMF 167898

*Description:* Shell (Fig. 3G) ovate-conical, larger specimen 1.86 mm high, 4.25 hardly convex whorls; aperture with straight outer lip and a distinct angle between parietal and palatal walls; the larger specimen had no varix, the smaller one a very inconspicuous varix close to outer lip; umbilicus a very narrow slit.

*Remarks:* The generic allocation has been confirmed by Boeters (1988). Both seminal receptacles are about equally long, the bursal duct is short, and the bursa copulatrix is a simple, slender sac. The penis has a distinct lobe pointing anteriorly in the middle of the left side; the penial tip tapers gradually and has a black spot in its right half. Conchologically, *B. h. heussi* is similar to its Portuguese "fellow-species" *B. lusitanica*. These species differ primarily in the convexity of the whorls and in that *B. lusitanica* has always a distinct varix. *Belgrandia h. heussi* is wider and has a higher aperture than *B. lusitanica* (see also Figs. 4, 5), but these differences are not significant after Bonferroni correction (Mann Whitney U-test). Anatomical differences may be the short proximal receptacle and the smaller penial lobe in *B. lusitanica*. However, Boeters (1988) has apparently investigated only one specimen of each sex in each species. More data would be desirable.

*Belgrandia heussi alcoaensis*
Boettger, 1963

*Belgrandia heussi alcoaensis* Boettger, 1963: 42

*Type Material:* holotype SMF 176900; paratypes SMF 176901 (14)

*Type Locality:* Rio Alcoa, Portugal

*Material Examined:* one paratype ex SMF 176901

*Description:* The single specimen investigated (Fig. 3H) is 1.9 mm high and has four basally keeled whorls, giving the shell the shape of an Asian temple; the outer lip is straight; no varix; umbilicus an open slit.

*Remarks:* The keel can be variably distinct according to the original description (Boettger, 1963). Otherwise, neither Boettger nor Boeters (1988) found further differences to the nominate subspecies. However, probably due to the keel *B. heussi alcoaensis* appears to be much wider, which is also reflected in the PCA (Fig. 5; Appendix 2). Unfortunately, only very few specimens of each subspecies were at my disposal, so that no statistical confirmation has been possible. However, *B. h. alcoaensis* is unambiguously diagnosable because of its keel. Its status as subspecies might even be questioned. Because I cannot add substantial new data, I refrain from changing its rank.

*Belgrandia ionica*
(Schütt, 1980)

*Remarks:* This species from the Greek island Corfu, originally described as *Litthabitella chilodia ionica* Schütt, 1980, has only recently and tentatively been attributed to *Belgrandia* by Bodon et al. (1999). Schütt's holotype turned out to be most likely a *Belgrandia,* while the paratypes from the Island of Levkas belong to *Litthabitella* Boeters, 1970. The description of *B. ionica* is very vague. Therefore, I refrain from a further treatment and discussion and refer to Schütt (1980) and Bodon et al. (1999) for more details.

## SPECIES ONCE ERRONEOUSLY ALLOCATED TO *BELGRANDIA*

Practically all European nominal species with one or more varices behind the outer lip have been attributed to *Belgrandia* at one time or another. However, Clessin (1882) realized that the formation of varices may not be restricted to *Belgrandia* and moved *B. guranensis* Paladilhe, 1870, *B. simoniana* Paladilhe, 1870[1], and *B. subovata* Paladilhe, 1876, to *Bythinella*. Later authors (e.g.,

[1]In fact. this name has been introduced by Moquin-Tandon (1856: 518) as *Bythinia marginata* var. *simoniana:* Paladilhe (1870) elevated its rank, and since then most subsequent authors ascribed the authorship to Paladilhe. Nevertheless, Moquin-Tandon's original combination frequently appears in the synonymy (e.g., Paladilhe, 1870; Clessin, 1882; Locard, 1882, 1893). Locard (1893) changed the name to *Belgrandia saint-simoniana* Paladilhe, 1870; Germain (1913, 1931) adopted Locard's name in the slightly altered version *B. saint-simoni,* but cited Moquin-Tandon as author.

Locard, 1893; Germain, 1913, 1931) did not follow Clessin. However, my own investigation (Bernasconi, in prep.) of the syntypes of *B. guranensis* and *B. simoniana* (both MHNG) confirmed Clessin's view as to these taxa. (His other reallocations cannot be followed.). The syntypes of *B. subovata* could not be traced, but the original description emphasizing a very blunt apex suggests that this species is a *Bythinella.*

Further species once assumed to belong to *Belgrandia* and later placed into other genera are *Cyclostoma vitreum* Draparnaud, 1801, and *B. cylindracea* Paladilhe, 1869. *Cyclostoma vitreum* has been identified as *Moitessieria* Bourguignat, 1863 (Boeters, 1969, 1972). Boeters (1998) has also recognized that *B. cylindracea* is a *Bythinella* and declared both *Belgrandia sequanica* Paladilhe, 1870, and *B. tricassina* Locard, 1893, synonyms. *Bythinella lanceolata* Locard, 1893, and *B. riparia* Locard, 1893, are treated as forms of *Bythinella cylindracea,* a category excluded from the provisions of the International Code of Zoological Nomenclature (Article 15.2, ICZN, 1999).

*Bithinia diaphana* Dupuy, 1849, was considered to be a synonym of *Belgrandia vitrea* (Draparnaud, 1805) by Germain (1931). Draparnaud's species has turned out to be a *Moitessieria* (see above), and *Paludina diaphana* Michaud, 1831, which is the original name—Dupuy is only the author of the combination *Bithinia diaphana*—belongs to *Bythiospeum* Bourguignat, 1882 (Bernasconi, 1985).

The seven fossil species from alluvia of the river Seine described by Bourguignat in 1869, *Belgrandia joinvillensis, B. desnoyersi, B. lartetiana, B. archaea, B. deshayesiana, B. edwardsiana,* and *B. dumesniliana,* all share a blunt apex (Bourguignat, 1869). The syntypes were not traceable, but Bourguignat (1869) used the same expression for the description of the apex of those seven species as Paladilhe (1869) for *B. cylindracea* (Paladilhe, 1869) and for *B. sequanica* Paladilhe, 1870 (Paladilhe, 1870), and Locard (1893) for *B. lanceolata, B. riparia,* and *B. tricassina,* that is, obtusus (Latin) or obtus (French), which mean obtuse, blunt, truncate. The syntypes of these five nominal species still exist (MHNG). They all have a blunt apex as it is typical for the genus *Bythinella* and have already been identified as such as stated above. Therefore, I consider also Bourguignat's seven fossil species, for which he in fact has introduced the name *Belgrandia,* to belong to *Bythinella.*

*Belgrandia bourguignati* de Saint-Simon, 1870, from Bourrassol may be a similar case. Also this species is rather a *Bythinella* judging form the original description (de Saint-Simon, 1870). Syntypes are not known. Germain (1931) treated it as a variety of *Belgrandia cylindracea,* which turned out to be a *Bythinella* (see above). This may be additional circumstantial evidence.

Again similar is the case of *Belgrandia nana* Sandberger, 1880, a fossil species from Great Britain, the syntypes of which are probably also lost. Sandberger (1880–1881) described the apex as blunt and identified *B. sequanica* as closest relative. Sandberger's figure (tab. XII, fig. 5, 5b) shows a shell with pointed apex. However, this discrepancy between description and illustration exists also in the original publications introducing the above listed French species. Hence, *B. nana* is probably also a *Bythinella.*

Another fossil British species was attributed to *Belgrandia* by Sandberger (1880–1881), *Paludina minuta* Strickland. This nominal species is listed as synonym of *B. marginata* by Wood (1850–1856) and found in a list in Murchison (1839). However, I have been unable to trace an original description by Strickland, and it is therefore likely that *P. minuta* is a *nomen nudum.* In addition, this species might also belong to *Bythinella* judging from the description given by Wood (1850–1856).

Bourguignat (1877) and later authors (e.g., Wagner, 1914) have also attributed a number of species primarily from the Balkan area with pupiform shell but lacking a varix to *Belgrandia.* Today, these species belong to *Belgrandiella* Wagner, 1928, and related or similar genera (Wagner, 1928; Radoman, 1983; Haase, 1994). They are not further discussed here nor included in Appendix 1.

### ***Belgrandia gfrast,*** nov. sp.

*Diagnosis: B. gfrast,* nov. sp., differs from all other congeners with a single varix on the body whorl by its unique shell shape. It is rather broadly conical, with a pointed apex and convex whorls. The proportion of shell height to shell width is 1.78 ± 0.08 (mean ± standard deviation). The peristome may be detached and the varix up to half a whorl behind the outer lip. The new species is further characterized by a wide lobe on the left

side in the distal half of the penis. An occasional second lobe opposite to the first one is smaller. Also unique is the wide visceral oviduct.

*Holotype:* NMB 11473 (Fig. 6)

*Paratypes:* MNHN (15 specimens), NHMW 90924 (15 specimens), NMB 11474 (> 50 specimens), ZSM 19990017-1999001724 (series of eight histological sections)

*Type Locality:* Origin of the Chenal des Sources (47°36.9'N, 7°32.3'E; 242 m above sea level) in the Petite Camargue, Alsace, France.

*Etymology:* Gfrast, used as noun in apposition, is Viennese dialect and describes – depending on the context – a charmingly or really impudent person. The new species is dedicated to my friend Kathrin Wunderle, who has been giving me a wonderful time since we met in Switzerland.

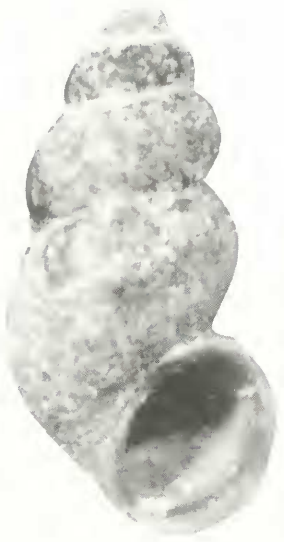

FIG. 6. Holotype (female) of *Belgrandia gfrast*, nov. sp. Shell height = 2.34 mm.

*Shell:* The shell is conical with up to 4.375 convex whorls, of which the protoconch comprises somewhat more than one whorl (Figs. 2G, 7, 8). Measurements are given in Table 1. Males and females cannot be distinguished by their shells. The aperture is oval and can be slightly detached from the penultimate whorl, leaving a narrow, but open umbilicus. The outer lip is orthocline, with an adapical sinus (Fig. 7B). There is a prominent varix mostly immediately, sometimes up to half a whorl behind the thin outer lip (Fig. 7B). The protoconch is pitted (Fig. 8B), while the teleoconch shows no structure except growth lines. The shell has no colour and the periostracum is light brown.

*Operculum:* The operculum is elongate-ellipsoidal, paucispiral, corneous, dark yellow, and its nucleus is submarginal and orange (Fig. 9A)

*Radula:* The radula (Fig. 9B) is six to seven times longer than wide. The ribbon is beneath the buccal mass, and the radular sac forms a simple U-shaped loop behind the buccal mass. The dorsal part of this loop contains, like the radula bolsters, black pigment. The central tooth is trapezoidal. Its basal tongue is as long as the lateral margins and broadly V-shaped with curved edges. The prominent pair of basal cusps arises from the lateral margins. The face of the lateral teeth is taller than wide and has a prominent basal projection. The lateral wing of the lateral teeth is much longer than the cutting edge. The cusps on the inner marginal teeth are slightly larger than on the outer marginal teeth. The cutting edge of the inner marginal teeth is longer than 25% of the total tooth length. The denticulation of the radula is described by the formula R:6-7 1 6-7/1 1, L: 5 1 5, M1: 24–28, M2: 28–32.

*Non-Genital Anatomy:* The epidermis is uniformly black, except for the mantle collar, the lips and the foot sole. The cephalic tentacles are black, with a white, ciliated line in the median (Fig. 10A) and a white tip. Black granules are found in the connective tissue of the head and foot. The snout is approximately as long as wide, slightly tapering and distally weakly lobate. There is no pallial tentacle, but a strongly ciliated sensory field on the right side of the mantle edge (Fig. 10B, C).

The ctenidium extends through about 75% of the mantle cavity and consists of six to eleven filaments, which are as broad as high. The osphradium is ellipsoid, more than two times longer than wide and lies somewhat behind the middle of the ctenidium. The hypobranchial gland is massively developed, and its distal end almost reaches the tip of the pallial oviduct.

Both supra- and suboesophageal connectives are long, and the oesophageal ganglia are not fused with the pleural ganglia. Cerebral, pleural and pedal ganglia contain black pigment granules.

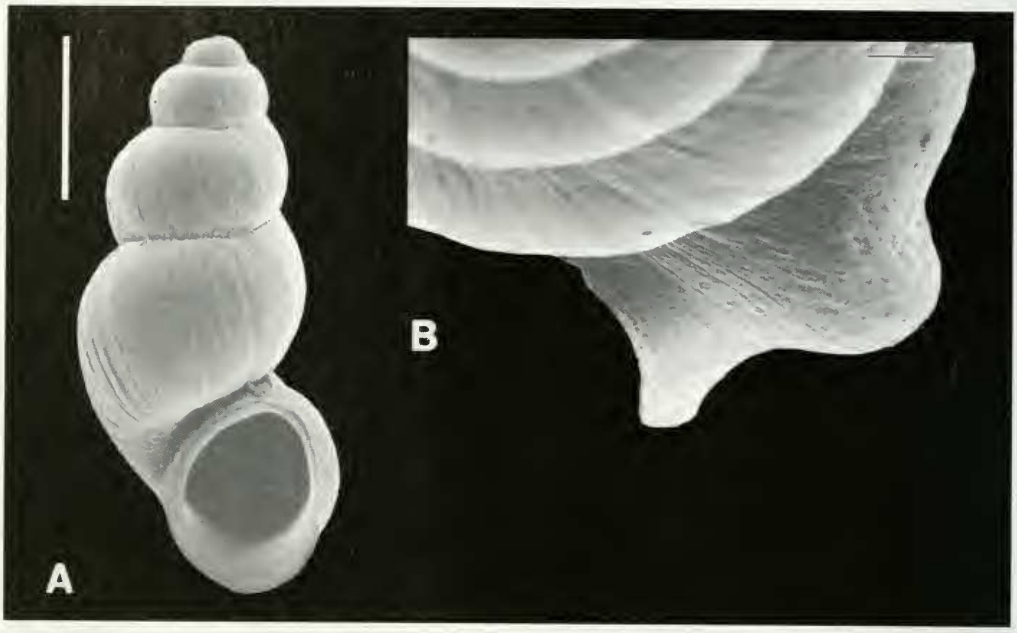


FIG. 7. Shell of *Belgrandia gfrast,* nov. sp. A, paratype; B, apical view of aperture of same specimen showing sinus and varix. Scale bars = 250 μm in A, 100 μm in B.

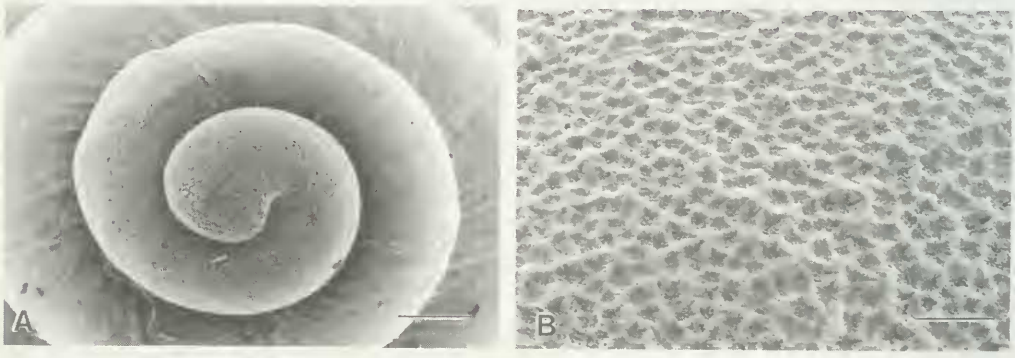


FIG. 8. Protoconch of *Belgrandia gfrast,* nov. sp. A, whole protoconch; B, surface structure. Scale bars = 100 μm in A, 10 μm in B.

In the proximal whorls, the digestive gland is a simple tube. Distally it has a series of lobes, the length of which increases with their distance from the apex. These lobes lie parallel to the columella and have their blind ends adapical (Fig. 11). The digestive gland has only a single opening into the stomach. The stomach has no coecum, and its anterior and posterior chambers are about equally long. The intestine coils around the style sac and runs straight along the pallial oviduct (Fig. 11) or the prostate, respectively. The anus lies behind the mantle edge.

*Female Reproductive System:* The ovary is a simple sac (Fig. 11) occupying more than 66% of the visceral coil behind the stomach and slightly overlaps the posterior chamber of the stomach. The visceral oviduct is exceptionally wide (Figs. 11–12). The renal oviduct is not pigmented and forms a simple loop of 270° lying against the bursa copulatrix. There

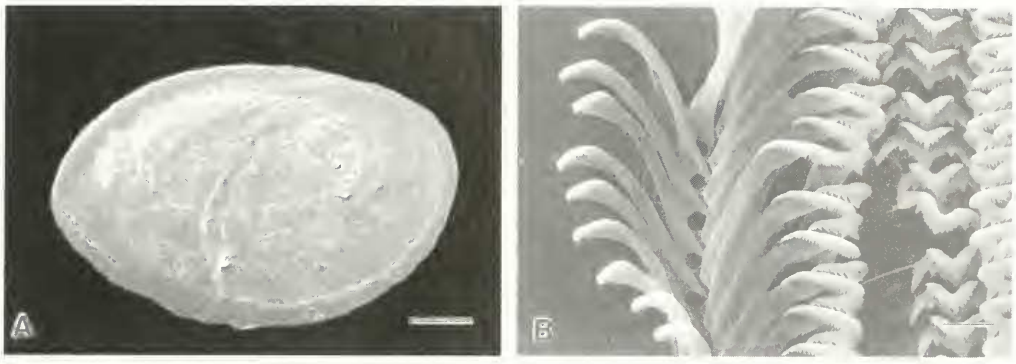

FIG. 9. Operculum and Radula of *Belgrandia gfrast*, nov. sp. A, inner side of operculum; B, left half of the radular ribbon, 9 transverse rows. Scale bars = 100 μm in A, 10 μm in B.

are two elongate seminal receptacles with short ducts. The proximal one arises from the proximal-most part of the straight section of the renal oviduct and bends around the ventroposterior edge of the bursa copulatrix. The distal receptacle is much smaller. It branches off at about the origin of the bursa copulatrix and lies against the latter. The bursa copulatrix is an elongate sac distally lying against the albumen gland. The posterior, blind end extends the albumen gland. The bursal duct lies on the longitudinal axis of the bursa and is considerably shorter than the latter. Both, capsule and albumen glands are bipartite. The posterior capsule gland and the anterior albumen gland are much shorter than the anterior capsule gland and the posterior albumen gland, respectively. The ventral channel forms a small vestibulum. The gonopore is a short slit shortly behind the distal end of the ventral channel (Fig. 12).

*Egg Capsules:* Egg capsules are lenticular and have an ellipsoid circumference. They are laid singly on the shells of their conspecifics, preferably, but not exclusively, along the sutures (Fig. 13). Whether eggs are deposited also on other firm substrates is not known.

*Male Reproductive System:* The testis has simple, vertical lobes. It begins almost at the tip of the visceral coil and distally covers the posterior chamber of the stomach. The posterior vas deferens coils immediately after it emerges from the middle region of the testis, forming a seminal vesicle. Before entering the prostate at its posterior end, the vas deferens makes an S-shaped loop. The prostate is bean-shaped. Its ventral surface is closed; there is no connection with the mantle cavity. The pallial vas deferens exits the prostate at its distal end. It is almost straight and has only weak musculature (Fig. 14). The resting penis is U-shaped. In extended condition it has parallel sides. It tapers only distal to the wide, muscular lobe on the left side in the distal half of the penis. Opposite to this left lobe there may be also a second, smaller lobe on the right side (Fig. 15). There is a black spot in the distal half of the penis. The pigment granula are in the connective tissue.

*Additional Observations:* Of 50 sexed snails 23 (46%) were males and 27 (54%) females. In the type locality, the density of adult snails was 6,400/$m^2$in October 1999. About 120 m downstream, the population density was 17,807 adults/$m^2$ (Mosimann, pers. comm.). The mantle cavity of each animal investigated anatomically contained peritrich ciliates of the genus *Trichodina* Ehrenberg, 1830, with diameters of about 60 μm.

*Remarks:* Shell morphology and anatomy of *B. gfrast* correspond well with the diagnosis of *Belgrandia*, so that the generic allocation of the new species is unambiguous. In order to confirm its status as a separate, hitherto undescribed species *B. gfrast* had to be compared to the known (nominal) species. According to multivariate analyses [PCA (Appendix 2), UPGMA] based on the nine morphometric parameters (Table 1), the most similar species were (Figs. 4, 5): *B. conoidea, B. gibberula, B. gibba*, and *B. heussi alcoaensis*. From these species, *B. heussi alcoaensis* was excluded from further statistical analyses, because only a single shell was available. Besides, it is clearly differentiated by its keel. In case of *B. gibberula*, it must be specified that the syntypes are rather remote from

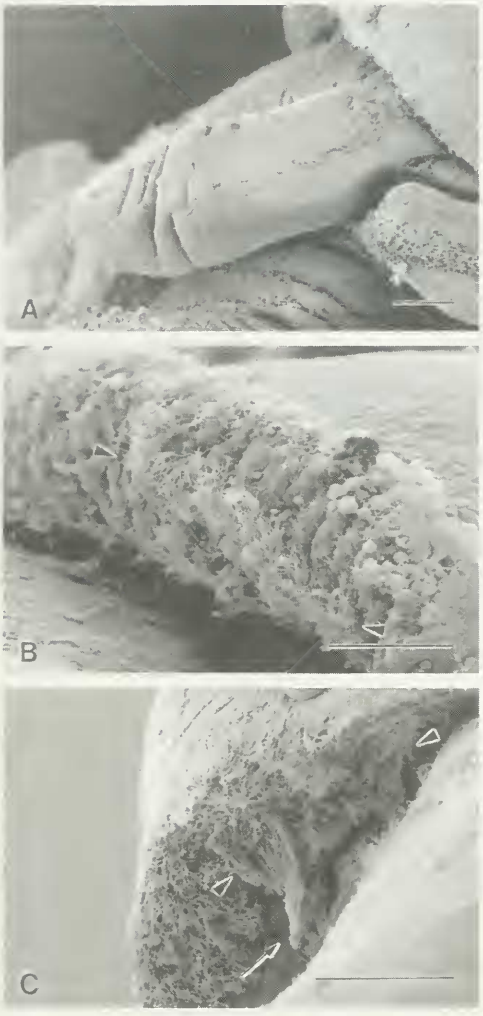


FIG. 10. Ciliation of *Belgrandia gfrast,* nov. sp. A, line of cilia on the right cephalic tentacle; B, C, ciliary sensory field on the right side of the mantle collar (between arrow heads). In C the arrow indicates a tuft of cilia, not a tentacle. Scale bars = 50 μm.

the other two samples ascribed to this species. A Kruskal-Wallis Test over all six samples was significant for all parameters (df = 5, $P \leq 0.0036$, Bonferroni corrected) but the ratio aperture height/aperture width. Omitting the syntypes of *B. gibberula,* significant differences were found only in the size parameters and the number of whorls (df = 4, $P \leq 0.027$, Bonferroni corrected). Of these remaining four samples compared to *B. gfrast,* only *B. gibba* is a name-bearing syntype series. As already mentioned, both samples ascribed to *B. gibberula* are very different from the syntypes of *B. gibberula.* The sample from St. Jean de Fos may represent a separate species, whereas *B. gibberula* from Hérault, which has up to three varices within the last 0.25 whorls, has affinities to *B. gibba. Belgrandia gfrast* is distinguished from both in that it has always one varix, which varies in position from closely behind to up to 0.5 whorls behind the outer lip. The syntypes of *B. gibba* have, in addition, a significantly smaller aperture, which is also smaller in relation to shell height (Mann Whitney U-Tests, $P < 0.05$, Bonferroni corrected) compared to *B. gfrast.* Anatomically, *B. gfrast* can readily be distinguished from *B. gibba* by its triangular penial lobe on the left side and the occasional presence of a small, right lobe. In *B. gibba,* there is only the left penial lobe, and this is smaller, pointed and directed anteriorly (Giusti & Pezzoli, 1980).

For a delimitation of *B. gfrast* from *B. varica,* I can only refer to its original description (Paget, 1854). Distinguishing features of *B. varica* are the much stouter shell, the peristome being never detached, and a single varix that is always closely behind the outer lip.

Also among the Italian nominal species, currently comprehensively revised by Cianfanelli, Bodon, Manganelli, & Giusti (pers. comm.) and why the following comparisons are kept to a minimum, none can be confused with the new species from the Petite Camargue Alsacienne. Generally, the single, variably positioned varix of *B. gfrast* is unique so far and allows its unambiguous identification even when compared to the less well-known, nominal species, that is, species lacking anatomical data, from Italy (Appendix 1). Currently, anatomical descriptions exist for only three nominal Italian species, *B. minuscola* (Paulucci, 1881), *B. caprai* Giusti, 1970, which is synonymized with *B. thermalis* (Linnaeus, 1767) by Bodon et al. (1995), and *B. mariatheresiae* Giusti & Pezzoli, 1972 (Giusti, 1970; Giusti & Pezzoli, 1972, 1980). Comparing only the genital anatomy, *B. caprai* appears to be very similar to *B. gfrast.* However, in *B. caprai* the cutting edge of the central radular tooth has fewer denticles, and the shell is much stouter and has an ample and unregularely shaped aperture (Giusti, 1970). Also, *B. mariatheresiae* has a rather conical, stout shell and, in addition, folds rather than varices, and its penis is much more slender with a single, round lobe on the

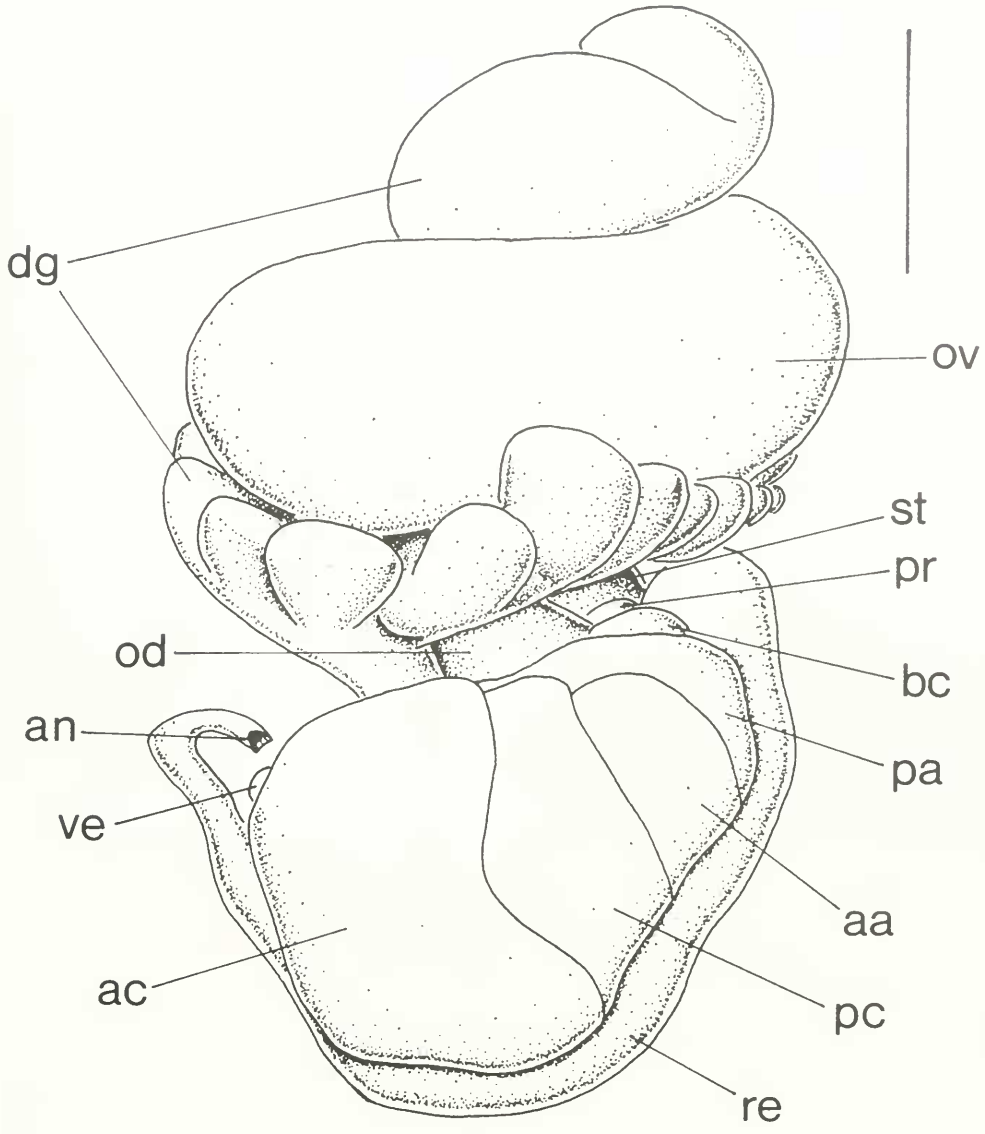


FIG. 11. Digestive and reproductive systems of a female of *Belgrandia gfrast*, nov. sp., foregut omitted. aa, anterior albumen gland; ac, anterior capsule gland; an, anus; bc, bursa copulatrix; dg, digestive gland; od, oviduct; ov, ovary; pa, posterior albumen gland; pc, posterior capsule gland; pr, proximal seminal receptacle; re, rectum; st, stomach; ve, vestibulum. Scale bar = 200 μm.

left side (Giusti & Pezzoli, 1972). *Belgrandia minuscola,* finally, lacks varices and penial lobes (Giusti & Pezzoli, 1980).

*Abiotic Characterization of the Type Locality:* The type locality of *B. gfrast* is the first of about 20 springs emerging on the edge of a low gravel terrace in the southwest of the Petite Camargue Alsacienne. These springs discharge into the 1.3 km long Chenal des Sources, which flows along the edge of the terrace towards north with 1–3 cm/s (Berger, 1993), primarily on gley. The springs are fed by water of brooks oozing away in the Sundgau west and southwest of the Petite Camargue Alsacienne (Schenker, 1992).

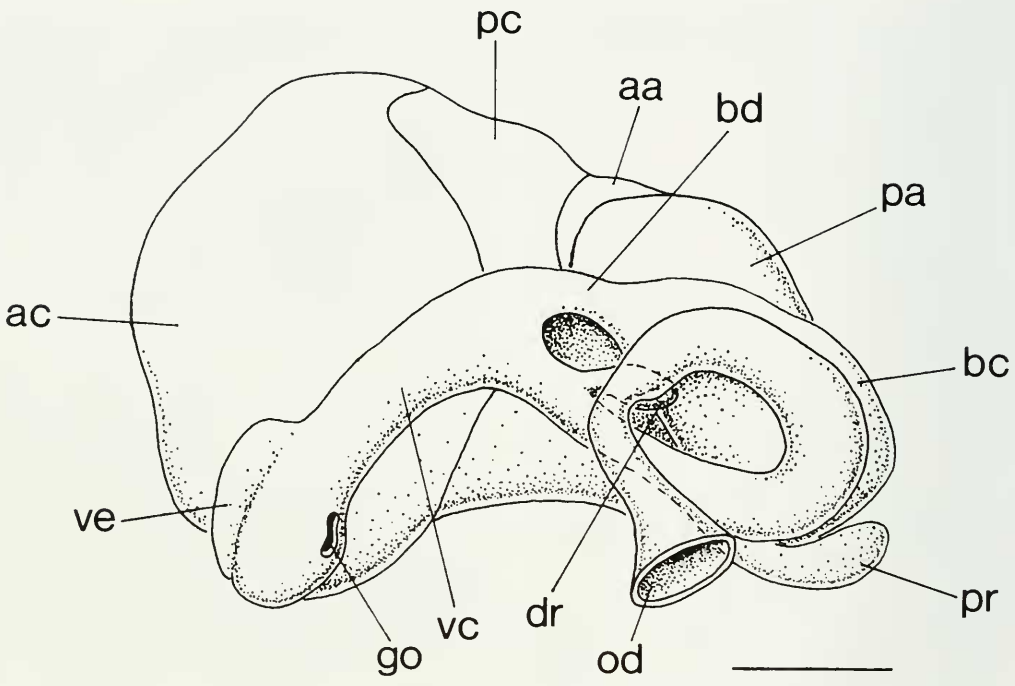


FIG. 12. Distal female genitalia of *Belgrandia gfrast*, nov. sp. aa, anterior albumen gland; ac, anterior capsule gland; bc, bursa copulatrix; bd, bursal duct; dr distal seminal receptacle; go, genital opening; od, oviduct; pa, posterior albumen gland; pc, posterior capsule gland; pr, proximal seminal receptacle; vc, ventral channel; ve, vestibulum. Scale bar = 100 μm.

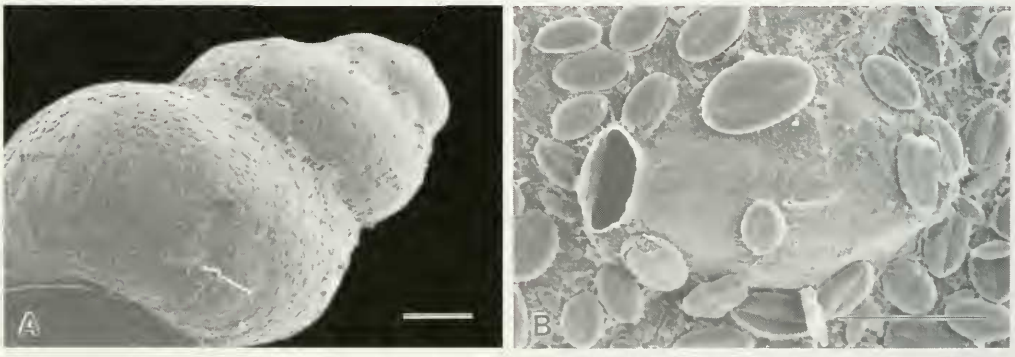


FIG. 13. Egg capsules of *Belgrandia gfrast*, nov. sp. A, on a subadult shell, arrow indicates egg capsule shown in B; B, single egg capsule. Scale bars = 200 μm in A, 50 μm in B.

The temperature was rather constant over the whole period of observation oscillating between 11.3°C and 12.3°C. The electric conductivity had its maximum in March with 810 μS/cm and steadily decreased until December 1990 down to 730 μS/cm. The pH varied between 6.80 and 7.19, with the lower values falling into the warmer period of the year. Ammonium was practically not detectable, while the concentration of nitrate was considerable with a minimum of 14.34 mg/l and a maximum of 37.48 mg/l. The concentration of phosphate was rather low during the year, with values between undetectable

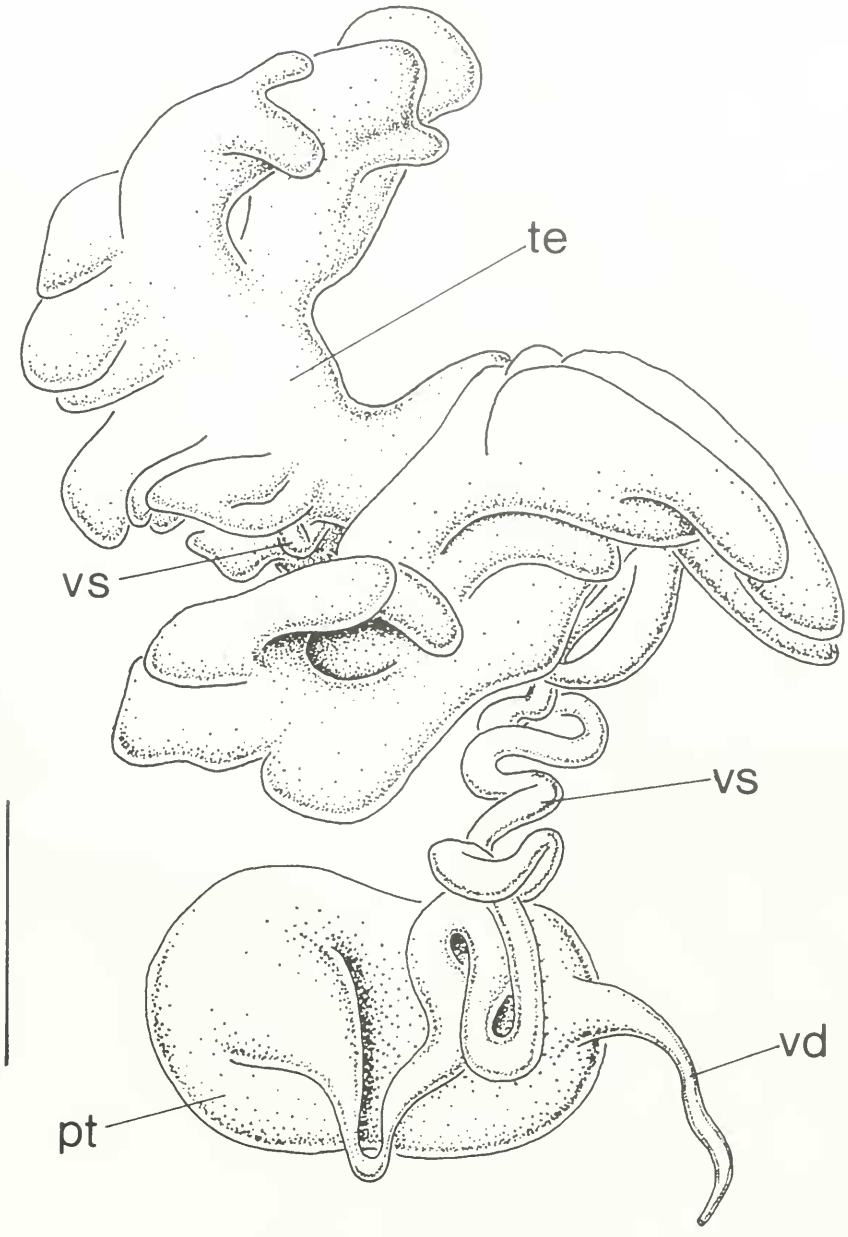


FIG. 14. Male genital system except penis of *Belgrandia gfrast*, nov. sp. pt, prostate; te, testis; vd, vas deferens; vs, vesicula seminalis. Scale bar = 200 μm.

and 0.06 mg/l. Only in late fall higher values up to 0.13 mg/l were measured. Chloride had its highest concentrations during the early months of the year, with a maximum of 44.1 mg/l, which decreased towards fall below 39 mg/l. The concentration of potassium oscillated between 1.1 mg/l and 5.1 mg/l over the period of observation with no detectable trend. The concentration of calcium was highest in winter and early spring, with a peak of 121.5 mg/l and decreased during the warmer period until fall to 48.4 mg/l. In November and

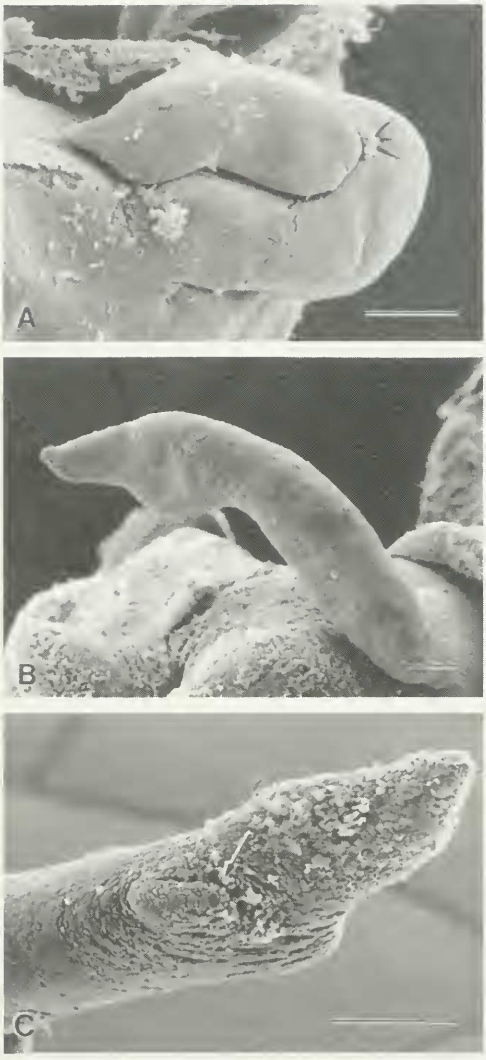


FIG. 15. Penis of *Belgrandia gfrast*, nov. sp. A, withdrawn; B, extended, only with left lobe; C, extended, arrow indicates small right lobe. Scale bars = 100 μm.

December, the concentration increased again. Magnesium, finally, showed an opposite trend with higher values during summer reaching up to 33.15 mg/l and lower concentrations in winter with a minimum of 8.65 mg/l.

## DISCUSSION

The latest extensive revision of the French malacofauna recognizes only five extant species as belonging to the genus *Belgrandia* (Germain, 1931), namely *B. gibba, B. saint-simoni* (= *B. simoniana,* see above), *B. marginata, B. vitrea* and *B. cylindracea.* The latter two were later shown to be a *Moitessieria* and a *Bythinella,* respectively (Boeters, 1969, 1972, 1998), and *Belgrandia saint-simoni* has also to be transferred to *Bythinella* as outlined above. The present account, on the other hand, recognizes eight French species, all of them extant. Three species occur on the Iberian Peninsula, and one each is from Croatia and Greece. *Belgrandia germanica* from eastern Germany is one of only three fossil species—there are two more fossil species from Italy described in Settepassi & Verdel (1965) (see Appendix 1)—being a true *Belgrandia* as far as can be judged from the original description (Sandberger, 1870–1875; Clessin, 1878b, 1882; the whereabouts of its syntypes are unknown, see above).

The discrepancy between Germain's (1931) and my conclusions is, of course, a consequence of our different approaches to analyze similarity and to interpret differences taxonomically. Compared with other groups of gastropods, the differences between congeneric hydrobiid species may appear rather negligible. However, considering that due to the miniaturization of hydrobiids the number of taxonomically useful characters is reduced (Hershler & Ponder, 1998), which means that only few characters can vary in the course of evolution, "slight" differences, be they quantitative or qualitative, gain comparatively higher taxonomic significance.

The morphological investigations have shown that there is considerable variance among French *Belgrandia.* This basic account should stimulate field studies, followed by anatomical studies and phylogenetic analyses, in order to learn more about the evolution and relationships of these species and, furthermore and probably even more important in our days, to evaluate the actual situation of this diverse fauna of spring snails, whose existence is only too often threatened through habitat destruction due to human activities (e.g., Ponder, 1994; Haase, 1996, Haase et al. in press; Hershler, 1996; Bouchet, 1997).

*Belgrandia gfrast* is the northern-most recent representative of the genus. The center of diversification of *Belgrandia* is southwest Europe (Giusti & Pezzoli, 1980; Germain, 1931; Boeters, 1988). The new species is thus fairly isolated from its recent congeners. However, during the Pleistocene, *Belgrandia* had appar-

ently a far wider distribution, reaching as far as eastern Germany (Sandberger, 1870–1875, 1880; Clessin, 1878b, 1882). Also the Dalmatian *B. torifera* appears to be remote from related species. But the Dalmatian spring snail fauna has more biogeographical affinities with western areas as indicated by the distribution of, for example, *Pyrgula annulata* (Linnaeus, 1767), which is sympatric with *B. torifera* (Schütt, 1961), and the genera *Islamia* Radoman, 1973, or *Orientalina* Randoman, 1978 (Schütt, 1961; Bodon et al. 1992; Bodon et al. 1994). The same holds for the Ionian Islands, where *B. ionica* occurs (Bodon et al., 1999). The distribution of the three Iberian species in the far west and the far east of the peninsula, respectively, suggests that there are more species to be discovered bridging this gap.

The phenetic analyses do not of course indicate systematic relationships. On the contrary, the high similarity of geographically remote species suggests convergent shell evolution rather than common ancestry, considering that the most common mode of speciation in crenobiontic hydrobiids is probably parapatric.

Whether *B. gfrast* and other *Belgrandia* species (*B. lusitanica* and *B* cf. *gibberula*) attach their egg capsules exclusively on shells of conspecifics or also on other hard substrata is not known. This behaviour, however, may probably be considered a further autapomorphy of *Belgrandia* paralleled by only few other, remotely related crenobiontic genera (e.g., Haase & Bouchet, 1998). Attaching eggs on conspecifics ensures that the eggs remain in their appropriate habitat in case the origin of a brook changes down- or upstream over a season depending on rainfall, provided the snails can follow these changes.

As probably the majority of crenobiontic hydrobiid species, *B. gfrast* lives in constantly cool and slowly running water (cf. Haase et al., in press). The water of the type locality is rich with calcium and magnesium, which reach similar concentrations as in natural carbonate brooks (Otto & Braukmann, 1983). However, the pH is much lower than in natural carbonate brooks, and the high values for conductivity and the high concentrations of chloride, nitrate and potassium indicate that the Chenal des Sources is fairly contaminated. The sources of this contamination are probably the nearby settlements and agriculture (Berger, 1993). A more comprehensive comparison of the autecology of *B. gfrast* with other species is hardly possible because of the lack of comparable data (Haase et al., in press). However, we begin to learn that crenobiontic hydrobiids do not necessarily indicate good water quality (Patzner, 1994).

Several epibiontic, peritrich ciliates of the genus *Trichodina* are known to be parasites, especially on fish (Görtz, 1996). But *Trichodina* is also found on a variety of invertebrates, among them several molluscs (e.g., van Banning, 1979; Raut, 1980; Basson & van As, 1992). Koval & Chernogorenko (1978) report a *Trichodina* sp. parasitizing on another hydrobiid gastropod, *Lithoglyphus naticoides* (C. Pfeiffer, 1828). Whether the ciliates encountered in the mantle cavity of *B. gfrast* are harmful to the snails or only commensalistic cannot be told from the sections.

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## APPENDIX 1.

TABLE 2. Nominal species attributed, at one stage or another, to *Belgrandia*. Species now attributed to *Belgrandiella* or related genera are excluded.

| Nominal species, subspecies, variety | Type locality | Allocation to *Belgrandia* and present allocation |
|---|---|---|
| *Turbo thermalis* Linnaeus, 1767 | Pisa, Italy | *Belgrandia thermalis* (Linnaeus, 1758)—Clessin (1882), Paulucci (1882); Cianfanelli et al., in prep. |
| *Cyclostoma vitreum* Draparnaud, 1801 | France | *Moitessieria (Spiralix) vitrea* (Draparnaud, 1801)—Boeters (1969, 1972) |
| *Cyclostoma gibbum* Draparnaud, 1805 | France | *Belgrandia gibba* (Draparnaud, 1805)—(Bourguignat, 1869) |
| *Paludina marginata* Michaud, 1831 | Foux de Draguignan, Var, France | *Belgrandia marginata* (Michaud, 1831)—Paladilhe (1870) |
| *Paludina minuta* Strickland, in Murchison, 1839 | Cropthorn, Great Britain | *Belgrandia minuta* (Strickland)—Sandberger (1880–1881)—probably a *nomen nudum*, present paper |
| *Paludina conoidea* Reynies, 1844 | Ardus sur l'Aveyron, près Montauban, France | *Belgrandia conoidea* (Reynies, 1844)—Falkner, Ripken & Falkner, in prep. |
| *Hydrobia varica* Paget, 1854 | Nice, Alpes Maritimes, France | *Belgrandia varica* (Paget, 1854)—Paladilhe (1869) |
| *Bythinia gibba* var. *uniplicata* Moquin-Tandon, 1856 | source of the river Lez near Montpellier | *Belgrandia gibba* var. *uniplicata* (Moquin-Tandon, 1856)—Clessin (1882); synonym of *Belgrandia gibba* (Draparnaud, 1805)—present paper |
| *Bythinia gibba* var. *marginata* Moquin-Tandon, 1856 | source of the river Lez near Montpellier | *Belgrandia gibba* var. *marginata* (Moquin-Tandon, 1856)—Clessin (1882); synonym of *Belgrandia gibba* (Draparnaud, 1805)—present paper |
| *Bythinia gibba* var. *aplexa* Moquin-Tandon, 1856 | source of the river Lez near Montpellier | *Belgrandia gibba* var. *aplexa* (Moquin-Tandon, 1856)—Clessin (1882); synonym of *Belgrandia gibba* (Draparnaud, 1805)—present paper |

TABLE 2. Continued.

| Nominal species, subspecies, variety | Type locality | Allocation to *Belgrandia* and present allocation |
|---|---|---|
| *Bythinia marginata* var. *simoniana* Moquin-Tandon, 1856 | near Cierp, France | *Belgrandia simoniana* (Moquin-Tandon, 1856)—Paladilhe, 1870; *Bythinella simoniana* (Moquin-Tandon, 1856)—(Clessin, 1882) |
| *Hydrobia moitessieri* Bourguignat, 1866 | source of the river Martinet near Montpellier, France | *Belgrandia moitessieri* (Bourguignat, 1866)—Bourguignat (1869) |
| *Bythinia saviana* Issel, 1866 | San Giuliano near Pisa, Italy | synonym of *Thermhydrobia thermalis* (Linnaeus, 1767)—Paulucci, 1878; *Belgrandia saviana* (Issel, 1866)—Clessin (1878c); synonym of *B. thermalis* (Linnaeus, 1767)—Clessin (1882); see also Cianfanelli, Bodon, Manganelli & Giusti in prep. |
| *Hydrobia lusitanica* Paladilhe, 1867 | Fonte das Lagrimas, Coimbra, Portugal | *Belgrandia lusitanica* (Paladilhe, 1867)—Paladilhe (1869) |
| *Belgrandia joinvillensis* Bourguignat, 1869 | Joinville-le-Pont, Val-de-Marne, France | *Bythinella joinvillensis* (Bourguignat, 1869)—present paper |
| *Belgrandia desnoyersi* Bourguignat, 1869 | Canonville, Val-de-Marne, France | *Bythinella desnoyersi* (Bourguignat, 1869)—present paper |
| *Belgrandia lartetiana* Bourguignat, 1869 | Joinville-le-Pont, Val-de-Marne, France | *Bythinella lartetiana* (Bourguignat, 1869)—present paper |
| *Belgrandia archaea* Bourguignat, 1869 | Joinville-le-Pont, Val-de-Marne, France | *Bythinella archaea* (Bourguignat, 1869)—present paper |
| *Belgrandia deshayesiana* Bourguignat,1869 | Joinville-le-Pont, Val-de-Marne, France | *Bythinella deshayesiana* (Bourguignat, 1869)—present paper |
| *Belgrandia edwardsiana* Bourguignat, 1869 | Canonville, Val-de-Marne, France | *Bythinella edwardsiana* (Bourguignat, 1869)—present paper |
| *Belgrandia dumenisliana* Bourguignat, 1869 | Canonville, Val-de-Marne, France | *Bythinella dumenisliana* (Bourguignat, 1869)—present paper |
| *Hydrobia paladilhi* Dubrueil, 1869 1869 | Frouzet near St. Martin de Londres, France | synonym of *Belgrandia gibberula* Paladilhe, 1869–Paladilhe (1870) |
| *Belgrandia cylindracea* Paladilhe, 1869 | environs of Amances, France | *Bythinella cylindracea* (Paladilhe, 1869)—Boeters (1998) |
| *Belgrandia bigorriensis* Paladilhe, 1869 | Bigorre, France | *Belgrandia bigorriensis* Paladilhe, 1869 |
| *Belgrandia gibberula* Paladilhe, 1869 | St. Guilhem le Désert, France | *Belgrandia gibberula* Paladilhe, 1869 |
| *Belgrandia guranensis* Paladilhe, 1870 | Guran near Cierp, France | *Bythinella guranensis* (Paladilhe, 1870)—Clessin (1882) |
| *Belgrandia sequanica* Paladilhe, 1870 | river Seine near Verrières | synonym of *Bythinella cylindracea* (Paladilhe, 1869)—Boeters (1998) |
| *Belgrandia bourguignati* de Saint-Simon, 1870 | Bourassol, France | *Bythinella bourguignati* (de Saint-Simon, 1870)—present paper |
| *Belgrandia subovata* Paladilhe, 1876 | Clausel, France | *Bythinella subovata* (Paladilhe, 1876)—Clessin (1882) |
| *Belgrandia occidentalis* Clessin, 1878 | Coimbra, Portugal | synonym of *Belgrandia lusitanica* (Paladilhe, 1867)—Clessin (1882) |
| *Belgrandia germanica* Clessin, 1878 | Weimar, Gräfentonna and Mühlhausen, Germany | *Belgrandia germanica* Clessin, 1878 |

TABLE 2. Continued.

| Nominal species, subspecies, variety | Type locality | Allocation to *Belgrandia* and present allocation |
|---|---|---|
| *Belgrandia bonelliana* de Stefani, 1879 | Sarteano, Italy | Cianfanelli et al., in prep. |
| *Belgrandia thermalis* var. *controversa* Del Prete, 1879 | Bozzano, Italy | synonym of *Belgrandia thermalis* (Linnaeus, 1767)—Bodon et al. (1995); Cianfanelli et al., in prep. |
| *Thermhydrobia thermalis* var. *minuta* Paulucci, 1880 | near Sesto, Italy | Cianfanelli et al., in prep. |
| *Belgrandia nana* Sandberger, 1880 | Mundesley, Great Britain | *Bythinella nana* (Sandberger, 1880)—present paper |
| *Hydrobia minuscola* Paulucci, 1881 | S. Agata Matese, Italy | *Belgrandia minuscola*—Giusti & Pezzoli (1980); Cianfanelli et al., in prep. |
| *Hydrobia minuscola* var. *curta* Paulucci. 1881 | Caramanico, Italy | Cianfanelli et al., in prep. |
| *Belgrandia targioniana* Clessin, 1882 | Firenze, Italy | Cianfanelli et al., in prep. |
| *Belgrandia delpretiana* Clessin, 1882 | Viareggio, Italy | synonym of *Belgrandia thermalis* (Linnaeus, 1767)—Bodon et al. (1995); see also Cianfanelli et al., in prep. |
| *Hydrobia boscae* Salvana 1887 | springs near Gandia, Spain | synonym of *Belgrandia* cf. *marginata*—Boeters (1988); *B. boscae*—present paper |
| *Belgrandia cazioti* Westerlund, 1890 | Les Angles, France | *Belgrandia cazioti* Westerlund (1890) |
| *Belgrandia cazioti* Locard, 1892 | quarter Champfleuri near Avignon, France | primary junior homonym of *Belgrandia cazioti* Westerlund, 1890, and probably synonym of *B. coutagnei*—present paper |
| *Belgrandia coutagnei* Locard, 1892 | quarter Champfleuri near Avignon, France | *Belgrandia coutagnei* Locard (1892) |
| *Belgrandia lanceolata* Locard, 1893 | river Seine near Verrières | synonym of *Belgrandia cylindracea* Paladilhe, 1869—Germain (1913); synonym (forma) of *Bythinella cylindracea* (Paladilhe, 1869)—Boeters (1998) |
| *Belgrandia riparia* Locard, 1893 | river Seine near Verrières | synonym (forma) of *Bythinella cylindracea* (Paladilhe, 1869)—Boeters (1998) |
| *Belgrandia tricassina* Locard, 1893 | river Seine near Verrières | synonym (forma) of *Bythinella cylindracea* (Paladilhe, 1869)—Boeters (1998) |
| *Belgrandia heussi heussi* C. Boettger, 1963 | Rio Liz, Portugal | *Belgrandia heussi heussi* Boettger, 1963 |
| *Belgrandia heussi alcoaensis* C. Boettger, 1963 | Rio Alcoa, Portugal | *Belgrandia heussi alcoaensis* Boettger, 1963 |
| *Belgrandia latina* Settepassi, in Settepassi and Verdel, 1965 | Valle del Liri, Latium, Italy | Cianfanelli et al., in prep. |
| *Belgrandia zilchi* Settepassi, in Settepassi and Verdel, 1965 | Ponte di Castelluccio, Latium, Italy | see Cianfanelli et al., in prep. |
| *Belgrandia caprai* Giusti, 1970 | Rosia, Toscana, Italy | synonym of *Belgrandia thermalis* (Linnaeus, 1767)—Bodon et al. (1995); Cianfanelli et al., in prep. |
| *Belgrandia mariatheresiae* Giusti & Pezzoli, 1972 | Fonte di S. Cassiano near Fabriano, Italy | Cianfaneli et al., in prep. |
| *Litthabitella chilodia ionica* Schütt, 1980 | Messongi river, Corfu, Greece | *Belgrandia ionica* (Schütt, 1980)—Bodon et al. (1999) |

## APPENDIX 2.
## PRINCIPAL COMPONENT ANALYSIS

The principal component analysis based on the correlation matrix of all nine shell parameters yielded eight principal components with positive Eigenvalues (Table 3). Principal components 1–3 represent 93.66% of the total variance. Therefore, the three dimensional ordination of the samples in Figure 5 represents fairly well the originally nine dimensional morphospace. PC1 is primarily composed of the size parameters. PC2 mainly represents the ratios sh/ah, sh/sw, which indicate shell shape, and the number of whorls. Two shape parameters, sw/aw and ah/aw, and aperture width have the highest weights on PC3.

TABLE 3. Principal component analysis based on a matrix of correlations of the shell parameters of Table 1. cv, cumulative variance in %; E, Eigenvalue; PC, principal component; v, variance in %; w, weights of parameters in Eigenvectors.

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 |
|---|---|---|---|---|---|---|---|---|
| E | 4.34200 | 2.95000 | 1.13700 | 0.40390 | 0.15770 | 0.00781 | 0.00085 | 0.00029 |
| v | 48.25 | 32.78 | 12.64 | 4.49 | 1.75 | 0.09 | 0.00 | 0.00 |
| cv | 48.25 | 81.02 | 93.66 | 98.15 | 99.90 | 99.99 | 100 | 100 |
| | w | w | w | w | w | w | w | w |
| sh | 0.44555 | 0.16659 | –0.18683 | –0.06913 | –0.24356 | –0.81054 | –0.11577 | 0.06170 |
| sw | 0.44319 | –0.20835 | –0.06515 | 0.17195 | –0.09382 | 0.28777 | –0.56142 | –0.07638 |
| ah | 0.44581 | –0.16978 | –0.15358 | –0.24710 | 0.00128 | 0.20837 | 0.13284 | –0.66924 |
| aw | 0.38565 | –0.24662 | –0.38925 | –0.06271 | 0.02411 | 0.25191 | 0.42380 | 0.62385 |
| W | 0.25847 | 0.43338 | –0.13050 | 0.29662 | 0.80005 | –0.00604 | 0.00638 | –0.01161 |
| sh/sw | –0.00279 | 0.55966 | –0.15731 | –0.31557 | –0.20449 | 0.33419 | –0.47157 | 0.24402 |
| ah/aw | 0.28457 | 0.16978 | 0.59988 | –0.61089 | 0.14339 | 0.03350 | 0.18808 | 0.09094 |
| sh/ah | 0.06477 | 0.55588 | –0.09126 | 0.27162 | –0.44021 | 0.18664 | 0.46435 | –0.23348 |
| sw/aw | 0.32496 | –0.01802 | 0.61301 | 0.51588 | –0.18720 | 0.07591 | –0.02715 | 0.17556 |